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POLLEN MORPHOLOGY OF MEXICAN ACANTHACEAE:
DIVERSITY AND SYSTEMATIC SIGNIFICANCE

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Diversity of pollen morphology is described for all 39 genera of Mexican Acanthaceae based on scanning electron microscopic study of 324 of the approximately 400 species of the family that are native or naturalized in the country. Although there is substantial variation in pollen morphology among the genera, species within most genera tend to be relatively conservative with respect to sculpturing elements such as the type, number, and position of apertures. Palynological diversity within the most speciose genus of Mexican Acanthaceae, *Justicia*, is as great as, or greater than, that recorded for the genus on a worldwide basis. Where possible or appropriate, pollen characters are used to assess the relative merits of two systematic classifications with respect to Mexican Acanthaceae. Some limitations of scanning electron microscopy for the characterization of pollen are noted.

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The remarkable diversity of pollen morphology in the Acanthaceae has been noted by virtually all those who have studied palynological aspects of the family. The early palynological observations of Acanthaceae by Radlkofer (1883) were extended by Lindau (1893, 1895), who recognized 11 pollen types in the family. Lindau (1895) based his widely used subfamilial classification of the family, in large part, on pollen morphology as encompassed by these types. The inadequacies of Lindau's pollen types for characterizing the observed palynological diversity in the family have been noted by subsequent workers (e.g., Bhaduri 1944; Bremekamp 1948; Scotland 1990a, 1991). More recent palynological studies that have considered a large number of genera of Acanthaceae (Raj 1961, 1973; Scotland 1990a), by necessity, have been based on only a few species per genus. Some limitations of broad, superficial palynological surveys of the family have been noted

(e.g., Figueiredo and Keith-Lucas 1996; Immelman 1987) and are further discussed below. Several comprehensive studies of pollen at the generic level have been completed recently (e.g., Figueiredo and Keith-Lucas 1996; Furness 1989, 1990, 1991, 1996; Hilsenbeck 1990), sometimes revealing considerable palynological diversity within a genus.

The present study attempts a comprehensive survey of all acanthaceous genera within a taxonomically diverse geographic region, Mexico. With about 400 species in 39 genera, Mexico comprises a center of diversity for the family with considerable endemism at both the generic and specific levels. Pollen of 324 species representing all 39 genera of Mexican Acanthaceae has been studied in order to: include palynological data in a forthcoming treatment of the family in Mexico; assist in classifying Mexican genera, particularly those endemic to the country or region; assess the usefulness of pollen observations

based solely on relatively simple SEM preparations in a regional geographic context; and add to the overall knowledge of acanthaceous pollen.

In other regional studies of Acanthaceae pollen, Rizzini (1947) surveyed pollen of many Brazilian genera and utilized pollen characters in distinguishing and classifying genera there; Petriella (1968) described and figured pollen of 30 species in 15 genera of Argentinean Acanthaceae and provided a key to genera based exclusively on palynological characters; and Muller, Schuller, Straka, and Friedrich (1989) described 26 different pollen morphological types among Acanthaceae in Madagascar and several islands of the Indian Ocean. The approach adopted here deemphasizes pollen types. The distinctions between types is often rather subjective (see under *Justicia* below) and a thorough study of pollen structure should be undertaken prior to their delimitation. Instead, comparative pollen descriptions are provided for each genus of Mexican Acanthaceae based on extensive sampling of species. Observed patterns and morphological correlations within and between suprageneric taxa are noted.

The subfamilial classification of Mexican Acanthaceae utilized here (Table 1) represents a compromise between that of Lindau (1895) and that of Bremekamp (1965). It maintains all of the taxa included by Lindau (1895) in the Acanthaceae but follows Bremekamp's (1965) arrangement of taxa with retinaculate capsules. A revised classification of Mexican Acanthaceae is currently being prepared based on morphological, cytological, palynological, and molecular data.

METHODS

Except where noted, pollen was observed and studied solely using scanning electron microscopy (SEM). Only morphological attributes (e.g., shape, size, aperture number and arrangement, surface sculpturing) are considered here. These attributes are the easiest to observe with SEM and have been used most frequently in previous palynological studies of Acanthaceae. Knowledge of the structure of grains is necessary, of course, for a complete characterization of pollen. Studies of pollen structure are much needed and undoubtedly will provide additional systematic information.

In all cases, pollen grains were removed individually from anthers on herbarium specimens with insect pins. They were mounted directly onto SEM stubs without any prior treatment such as acetolysis. Walker and Doyle (1975) noted that method and length of pollen preparation can affect pollen size and can cause the shape of grains to vary considerably as well. Hanks and Fairbrothers (1970) discussed specific effects of various preparation techniques on pollen of Fagaceae. The simple procedure noted above was used because SEM images of untreated pollen have been shown to portray more accurately the natural shape and dimensions of the grains (Daniel 1983a:13) and the procedure does not remove the apertural surfaces which can contain important systematic data. Differences in size and/or shape between acetolyzed and unacetolyzed pollen of Acanthaceae have been noted by Daniel (1983a, 1986a) and Valsaladevi and Mathew (1989). Immelman (1987) reported that no significant differences were found between acetolyzed and unacetolyzed pollen of two species of *Justicia* from southern Africa. Balkwill (1985) found that untreated pollen of Acanthaceae provided better results with SEM than variously treated pollen.

Photographs of appropriate grains representing each species were made to document the pollen characteristics observed. Measurements, such as lengths of polar (P) and equatorial (E) axes, were taken directly from the photographs. The pollen figures depicted here were made by scanning the photographic negatives into computer files, adjusting brightness and contrast levels, cleaning backgrounds, and configuring the individual images into plates.

Data from all species within a genus were pooled to formulate the generic descriptions below. In these descriptions, the name of the genus is followed by the number of species examined/the number of species of the genus in Mexico/the number of species in the genus. Pollen figures are cited at the end of the descriptions. Generic discussions (palynological variation, systematic considerations, etc.) follow the descriptions and include references to previously published images of pollen of Mexican species. All species and collections sampled are listed in the Appendix. Most of the specimens representing these collections are deposited at ASU, CAS, or MICH.

Terminology in the descriptions generally follows that of Walker and Doyle (1975). To the sculpturing elements described by them, the prefix "micro-" is sometimes added to characterize very small sculpturing elements (especially when a clear dichotomy in size of sculpturing elements is present). The term "bireticate" is used for pollen with a reticulate exine in which the lumina appear foveolate to microreticulate. In most instances, this microreticulum would appear to result from the visibility of the columellae (or collumellar branches), in side view, below the muri. For compound apertures, indication that the width of the colpi barely exceeds the diameter of the ora means that it is less than twice the diameter of the ora. Elongate and presumably harmomegathic furrowlike indentations in the exine between compound apertures (i.e., in the interapertural regions or mesocolpia) are referred to as pseudocolpi. The terminology used to describe the apertural regions in *Justicia* is presented and discussed under that genus.

All currently recognized genera of Mexican Acanthaceae were studied. Two other genera, *Pachystachys* Nees and *Geissomeria* Lindl., each based on a single collection from the nineteenth century, have been treated as occurring in Mexico. They are not included here. The sole species of *Pachystachys* known from Mexico was excluded by Wasshausen (1986) pending further collections to establish its generic affinities. The identity of the only species of *Geissomeria* described from Mexico is currently under study.

PALYNOLOGICAL DESCRIPTIONS AND DISCUSSIONS

Anisacanthus 7/8/ca. 18. Pollen euprolate to perprolate (P:E = 1.4–2.4), 3-colporate, 6-pseudocolpate, P = 52–97 μ m, E = 35–46 μ m; polar outline subtriangular to triangular; colpi fusiform, nearly as long as P, 8–9 μ m wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate to verrucate; pseudocolpi 2 per mesocolpium, shorter than or nearly as long as colpi, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces microverrucate to verrucate; interapertural surfaces (exclusive of pseudocolpi) rugulate to reticulate (reticulum homobrochate) to bireticate. Fig. 8f.

TABLE 1. Subfamilial classification of Mexican Acanthaceae.

Subfamily Thunbergioideae	<i>Thunbergia</i>
Subfamily Mendoncioideae	<i>Mendoncia</i>
Subfamily Nelsonioideae	<i>Elytraria, Nelsonia, Staurogyne</i>
Subfamily Acanthoideae	Tribe Aphelandreae
	<i>Aphelandra, Holographis, Stenandrium</i>
Subfamily Ruellioideae	Tribe Trichanthereae
	<i>Bravaisia, Sanchezia</i>
	Tribe Louteridioae
	<i>Louteridium</i>
	Tribe Lepidagathideae
	<i>Lepidagathis</i>
	Tribe Ruellieae
	Subtribe Barleriinae
	<i>Barleria, Lophostachys</i>
	Subtribe Blechiniae
	<i>Blechum</i>
	Subtribe Hygrophilinae
	<i>Hygrophila</i>
	Subtribe Petalidiinae
	<i>Dyschoriste</i>
	Subtribe Ruelliinae
	<i>Ruellia</i>
	Tribe Justicieae
	Subtribe Justiciinae
	<i>Justicia</i>
	Subtribe Isoglossinae (as "Rhytiglossinae" in Bremekamp, 1965)
	<i>Stenostephanus</i>
	Subtribe Odontoneminae
	<i>Anisacanthus, Aphanosperma, Carlowrightia, Chalarothyrsus, Chileranthemum, Dicliptera, Gypsacanthus, Henrya, Hoverdenia, Hypoestes, Mexacanthus, Mirandea, Odontonema, Pseudacanthemum, Schaueria, Spathacanthus, Tetramerium, Yeatesia</i>
	Genera Incertae Sedis
	<i>Poikilacanthus</i>

This American genus has centers of distribution in Mexico and South America. Pollen of Mexican *Anisacanthus* is typical of that usually encountered in the Odontoneminae. Most of the palynological variation noted among species of Mexican *Anisacanthus* pertains to shape and size of the grains.

Aphanosperma 1/1/1. Pollen euprolate to perprolate (P:E = 1.5–2.3), 3-colporate, 6-pseudocolpate, P = 39–50 μm , E = 21–27 μm ; polar outline subtriangular, poles sometimes with a 3-armed aperturelike indentation in the exine, arms aligned with colpi; colpi fusiform, nearly as long to as long as P, 2–6 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate to verrucate; pseudocolpi 2 per mesocolpium, equaling to longer than colpi, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces psilate; interapertural surfaces (exclusive of pseudocolpi) reticulate, reticulum homobrochate. Figs. 7d, e; 8e.

Aphanosperma is a unispecific genus, endemic to northwestern Mexico, with flowers similar to those of some species of *Carlowrightia*, but with capsules unique in the Odontoneminae. Its pollen is typical for Odontoneminae except for the presence of polar, aperturelike indentations in plants from one region of its range (see additional figures in Daniel 1988a, 1997). Plants from southern peninsular Baja California have this polar feature whereas plants from mainland Mexico do not. Wet preparations of pollen of *Aphanosperma* have been reported as having P = 29–39 μm , E = 25–34 μm , and P:E = 1.1–1.4 (Daniel 1988a).

Aphelandra 12/12/ca. 175. Pollen subprolate to perprolate (P:E = 1.3–2.4), 3-colpate, P = 36–66 μm , E = 21–44 μm ; polar outline circular to subtriangular, poles sometimes with a 3-armed aperturelike indentation in the exine, arms alternate with colpi; colpi fusiform or linear or hourglass shaped, as long or nearly as long as P, 1–6 μm wide at equator, sometimes fused at poles (i.e., syntricolpate), sometimes bifurcate near poles, sometimes with a \pm prominent and swollen margin, surfaces psilate to verrucate to gemmate to rugulate; interapertural surfaces foveolate to fossulate to gemmate-psilate to rugulate to reticulate, reticulum homobrochate to heterobrochate with larger lumina positioned equatorially (especially near colpi). Fig. 2a, c.

Aphelandra is neotropical in distribution. Wasshausen (1975) surveyed pollen of 60 species of *Aphelandra* and noted some palynological diversity among them. He further noted that the pollen types he recognized do not correlate well with macromorphological features used to distinguish the species. Daniel (1991a) described and figured palynological features of the Mexican species. Pollen of Mexican *Aphelandra* is generally consistent with that found elsewhere in the genus (McDade 1984; Wasshausen 1975, 1996) and is similar to that of other Mexican Aphelandreae. Pollen of a single Mexican collection from Oaxaca that otherwise greatly resembles *A. gigantiflora* is unique among species of the genus studied to date. It has a pseudocolpal ellipse in each mesocolpium (see figures in Daniel 1991a) and lacks the polar, aperturelike indentations of *A. gigantiflora*. The taxonomic status of this collection remains to be determined.

Barleria 1/1/80–250. Pollen spherical to subprolate (P:E = 1.0–1.3), 3-colporate to 3-colpoidate, P = 74–109 μm , E = 73–87 μm ; polar outline subtriangular; colpi sometimes \pm indistinct, sublinear to subfusiform, ca. 0.4–0.7 times as long as P, 6–17 μm wide at equator, not to barely exceeding or ca. 2 times diameter of ora in width, surfaces subspsilate to verrucate; interapertural surfaces coarsely reticulate, reticulum \pm heterobrochate, muri psilate, lumina psilate to verrucate to baculate, those adjacent to colpi largest. Fig. 5e, f.

Only one species, *B. oenotheroides*, of this primarily paleotropical genus occurs in the New World. Raj (1961) interpreted the apertures in *Barleria* as pores. I interpret them as compound apertures, as did Scotland (1990a). The infrafamilial relationships of *Barleria* have been controversial since Bentham and Hooker's (1876) placement of the genus in the tribe Justiceae (cf. Bremekamp 1965; Lindau 1895; Natarajan 1957). Raj (1961) and Daniel (1993a) concluded that its relatives include *Lepidagathis* and *Lophostachys*, both of which have similar pollen (see *Lophostachys*). Scotland, Endress, and Lawrence (1994) noted that a similar, and unusual among Acanthaceae, aestivation pattern of the corolla is common to these genera as well.

Blechnum 2/2/ca. 8. Pollen oblate spheroidal to euprolate (P:E = 0.9–1.4), 3-syncolporate, P = 40–57 μm , E = 35–59 μm ; polar outline subcircular to circular; colpi fusiform, as long as P,

fused at poles, 5–10 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces verrucate to gemmate; interapertural surfaces finely (i.e., longest axis of lumina ca. 0.4–1.3 μm) to coarsely (i.e., longest axis of lumina ca. 5–14 μm) reticulate, reticulum homobrochate, muri subspsilate to microverrucate, lumina psilate to verrucate. Figs. 5h; 11g.

This American genus of fewer than 10 species is represented in Mexico by *B. pyramidatum* and *B. grandiflorum*. Differences in exine sculpturing between these two species were discussed and figured by Daniel (1995a), who also noted pollen with intermediate sculpturing in a Central American species, *B. costaricense* Oerst. Pollen of another Central American species, *B. panamense* Lindau (*Mass & Dressler 663*) is also intermediate in sculpturing between them. Based on this limited sampling, it would also appear that grains of *B. pyramidatum* ($P = 40\text{--}49 \mu\text{m}$) are smaller than those of *B. grandiflorum* ($P = 57 \mu\text{m}$).

All species of the genus examined to date are syncolporate (Daniel 1995a; Erdtman 1952; Raj 1961; Ramamoorthy and Hornelas U. 1988; Scotland 1990a). Polar fusion of colpi is encountered elsewhere among Mexican Acanthaceae (e.g., *Aphelandra*, *Carlownrightia*, *Justicia*, *Pseuderanthemum*) as an incidental or species-specific part of palynological variation within a genus. In *Blechnum*, polar fusion of the colpi appears to be a fixed generic characteristic.

Bremekamp (1965) treated *Blechnum* as constituting a subtribe within the Ruellieae. Based on several macromorphological characteristics, the genus is similar to *Ruellia*. Features of the capsules and pollen, however, readily separate these genera (Daniel 1995a).

Bravaisia 3/3/3. Pollen globose-oblong to globose-elongate (longer apertural axis: interapertural axis = 1.5–2.1), 2-colporate, polypseudocolpate, sculptural features of one face $\pm 90^\circ$ out of phase with those of opposite face, longer apertural axis = 50–77 μm , shorter apertural axis = 48–70 μm , interapertural axis = 34–56 μm , apertural face subcircular to circular in outline. interapertural face elliptic to broadly elliptic in outline; colpi \pm linear to fusiform, nearly as long as axes of apertural faces, 3–7 μm wide near ora, surfaces verrucate; pseudocolpi 10–12 per aper-

tural face, of varying lengths, some fusing near periphery of grain, oriented in \pm same direction as colpi (i.e., perpendicular to one another on opposite aperturate faces), some appearing to encircle pollen in interapertural view (i.e., dividing the 2 identical but skewed halves of the grain), surfaces verrucate; exine between colpi divided into bands by pseudocolpi, \pm prominently protruding (liplike) on both sides of colpi at ora, bands psilate with a single row of foveolae down the center, longest axis of foveolae 0.2–2.7 μm . Fig. 3b, c.

The distribution of this neotropical genus is centered in southern Mexico and northern Central America. Pollen of all species (see figures in Daniel 1988b) is similar except that grains of the larger flowered species, *B. grandiflora*, are about 1.5 times longer (i.e., longer apertural axis) than those of the other two species. In the two samples of this species that were studied, most of the pollen was collapsed (see Daniel 1988b). Because of the unusual symmetry of the exine sculpturing, there are no clear distinctions between polar and equatorial axes in isolated pollen grains (i.e., what would appear to be the polar axis on one apertural face would appear to be the equatorial axis on the opposite face). Vasanthy and Pocock (1986) studied pollen of two species of *Bravaisia* and described its unusual form as “striate and rotationally symmetric.” Daniel (1988b) referred to this type of pollen as “loxodicolporate.” All Trichanthereae share this pollen type. Vasanthy and Pocock (1986) discussed possible origins for this type of pollen and noted similarities to anomalous grains of the Old World genus *Strobilanthes* Blume (as *Nilgirianthus* Bremek.) in the Strobilantheae.

Carlownrightia 23/23/24. Pollen prolate spheroidal to perprolate ($P:E = 1.1\text{--}2.2$), 3-colporate, 6-pseudocolpate, $P = 32\text{--}51 (-73) \mu\text{m}$, $E = 18\text{--}39 \mu\text{m}$; polar outline subtriangular to triangular; colpi fusiform, nearly as long as P , 2–8 μm wide at equator, not to barely exceeding diameter of ora in width, rarely fusing at one or both poles (3-syncolporate), surfaces microverrucate to verrucate; pseudocolpi 2 per mesocolpium, shorter than or as long as colpi, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces subspsilate to microverrucate; interapertural surfaces (exclusive of pseudocolpi) rugulate to reticulate

(reticulum homobrochate) to bireticate. Fig. 8c.

All but one species of this New World genus occur in Mexico. Pollen of *Carlowrightia* (see figures in Daniel 1981, 1983a, 1997) is similar to that of most other Mexican Odontoneminae. Most of the palynological variation noted within the genus results from differences in size and shape of grains. Daniel (1983a) noted that in wet preparations of *Carlowrightia* pollen $P = 30\text{--}63\ \mu\text{m}$, $E = 20\text{--}43\ \mu\text{m}$, and $P:E = 1.1\text{--}2.0$.

Chalarothyrsus 1/1/1. Pollen euprolate ($P:E = 1.8\text{--}1.9$), 3-colporate, 6-pseudocolpate, $P = 54\text{--}59\ \mu\text{m}$, $E = 30\text{--}34\ \mu\text{m}$; polar outline subtriangular to subcircular; colpi fusiform, nearly as long as P , $5\ \mu\text{m}$ wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate to verrucate; pseudocolpi 2 per mesocolpium, as long as colpi, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces not seen; interapertural surfaces (exclusive of pseudocolpi) reticulate, reticulum homobrochate. Fig. 8a.

Chalarothyrsus is endemic to Mexico. The genus was placed in the Asystasiae by Lindau (1904), the "typical representatives" of which were included in the Odontoneminae by Bremekamp (1965). Its pollen is similar to that usually encountered in that subtribe. The presence of four fertile stamens in *Chalarothyrsus* and *Spathacanthus* (also treated by Lindau in the Asystasiae) contrasts with other Mexican members of Bremekamp's Odontoneminae which have only two fertile stamens.

Chileranthemum 3/3/3. Pollen oblate spheroidal to perprolate ($P:E = 0.9\text{--}2.2$), 3-colporate, 6-pseudocolpate, $P = 31\text{--}58\ \mu\text{m}$, $E = 26\text{--}40\ \mu\text{m}$; polar outline subcircular (with prominent constrictions at pseudocolpi) to circular; colpi fusiform, nearly as long as P , $1\text{--}9\ \mu\text{m}$ wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate to verrucate; pseudocolpi 2 per mesocolpium, shorter than or as long as colpi, often fusing near poles thereby forming pseudocolpal ellipses in mesocolpia, surfaces subsilate to microverrucate; interapertural surfaces (exclusive of pseudocolpi) (subrugulate to) reticulate, reticulum homobrochate. Fig. 7i.

This genus is known only from Mexico. The questionable generic status of *Chileranthemum*

and several of its relatives in the Odontoneminae was discussed by Daniel (1995b). Pollen of *Chileranthemum* (see figures in Daniel 1993b) is similar to that of most other Mexican Odontoneminae and therefore does not assist in delimiting this genus.

Dicliptera 13/ca. 18/ca. 150. Pollen euprolate to perprolate ($P:E = 1.4\text{--}2.3$), sometimes slightly hourglass shaped due to a slight equatorial constriction, 3-colporate, 6-pseudocolpate, $P = 38\text{--}76\ \mu\text{m}$, $E = 22\text{--}34\ \mu\text{m}$; polar outline subtriangular; colpi fusiform, nearly as long as P , $2\text{--}6\ \mu\text{m}$ wide at equator, not to barely exceeding diameter of ora in width, surfaces subsilate to microverrucate; pseudocolpi 2 per mesocolpium, nearly to as long as colpi, sometime fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces subsilate to microverrucate; interapertural surfaces (exclusive of pseudocolpi) reticulate (reticulum \pm homobrochate) to bireticate. Fig. 7a.

Dicliptera is pantropical in distribution. The apparent difference in base chromosome number between New and Old World species of the genus (Daniel and Chuang 1993; Daniel et al. 1990) is not reflected by differences in pollen. Pollen of those species of *Dicliptera* examined (e.g., see figures in Daniel 1997) resembles that reported for Old World species (Balkwill 1985; Raj 1961; Scotland 1990a) as well as that of most other Mexican Odontoneminae.

Dyschoriste 15/ca. 20/ca. 75. Pollen subprolate to perprolate ($P:E = 1.2\text{--}2.5$), 3-colporate, irregularly polypseudocolpate, $P = (38\text{--}) 43\text{--}85\ \mu\text{m}$, $E = 26\text{--}38\ \mu\text{m}$; polar outline circular; colpi fusiform, ca. $1/3\text{--}2/3$ as long as P , $1\text{--}4\ \mu\text{m}$ wide at equator, not to barely exceeding diameter of ora, sometimes oblique (due to spiral/twisting of exine), surfaces not seen; pseudocolpi 4–12 per mesocolpium, mostly longer than colpi, often unequal in length, sometimes spiral/twisted, surfaces subsilate to microverrucate; exine between colpi divided into bands by pseudocolpi, \pm prominently protruding (liplike) on both sides of colpi at ora, bands densely microverrucate to microechinate and often microfoveolate to microfossulate. Figs. 4a–c; 11e.

Dyschoriste occurs in various parts of the world. Furness (1995) studied pollen of primarily African species of *Dyschoriste* and recognized a single basic pollen type in the genus with numerous subtypes based on the number of

pseudocolpi present. Among Mexican taxa, variation was noted in grain shape and size, number of pseudocolpi (the number often varying within a collection or on individual grains), and density of the supracteal sculpturing elements. Otherwise, pollen of Mexican species (see figures in Daniel 1990a, 1996, 1997) is relatively uniform and is entirely consistent with that described from other parts of the world (Furness 1995). Furness (1995) noted palynological similarities between *Dyschoriste* and the African genus *Chaetacanthus* Nees. Among other Mexican Rutellieae, pollen of *Dyschoriste* is most similar to that of *Hygrophila*, but differs by its three (vs. four) colpi, shorter colpi, and supracteal sculpturing.

Elytraria 4/4/ca. 15. Pollen euprolate to perprolate (P:E = 1.5–2.0), 3-colpate, P = 42–52 μm , E = 25–31 μm ; polar outline subtriangular to circular; colpi narrowly linear or fusiform, nearly as long as P, 1–7 μm wide at equator, surfaces subsilate (at least partially) to irregularly microechinate or verrucate; interapertural surfaces finely (i.e., longest axis of lumina ca. 0.3–1.9 μm) reticulate, reticulum \pm homobrochate, muri microverrucate to microbaculate to microechinate. Figs. 1g, h; 11b.

The 15 or so species of this genus are distributed in the tropics and subtropics of both Old and New Worlds. Scotland (1990a) noted colpate pollen in two New World species (including *E. imbricata*) and one Old World species and colpate pollen in an Old World species. Roubik and Moreno P. (1991) noted colpate pollen in *E. imbricata*. Endoapertures (ora) were not observed in SEM preparations of pollen of Mexican *Elytraria*.

The taxonomic affinities of the Nelsonioideae are not fully resolved. They have been treated as part of the Scrophulariaceae (e.g., Bremekamp 1965) and as a distinct family (Sreemadhavan 1977). Pollen of Mexican *Elytraria* (see figure in Daniel 1997) differs from that of other Mexican Nelsonioideae by its larger size and minute supracteal gemmae or echinae.

Gypsacanthus 1/1/1. Pollen subprolate (P:E = 1.2), 3-colporate, 6-pseudocolpate, P = 28–31 μm , E = 24–26 μm ; polar outline circular; colpi fusiform, nearly as long as P, 6 μm wide at equator, barely exceeding diameter of ora in width, surfaces microverrucate to verrucate to gemmate; pseudocolpi 2 per mesocolpium, shorter

than colpi, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces microverrucate; interapertural surfaces (exclusive of pseudocolpi) reticulate (reticulum homobrochate) to bireticulate. Fig. 7g.

Gypsacanthus is endemic to arid regions in southern Mexico. Pollen of *Gypsacanthus* studied and figured by Lott et al. (1984) is euprolate (P:E = 1.7), somewhat larger (P = 46 μm), and triangular in polar outline, but otherwise resembles that described here. The genus was included in subtribe Odontoneminae (Lott et al. 1984) in which this type of pollen is common.

Henrya 2/2/2. Pollen euprolate to perprolate (P:E = 1.7–3.0), sometimes slightly hourglass shaped due to a slight equatorial constriction, 3-colporate, 6-pseudocolpate, P = 50–71 μm , E = 25–32 μm ; polar outline triangular; colpi elliptical, nearly as long as P, 8–9 μm wide at equator, 2.0–2.7 times diameter of ora in width, surfaces densely verrucate to gemmate, verrucae or gemmae sometimes microverrucate; pseudocolpi 2 per mesocolpium, shorter to longer than colpi, surfaces not seen; interapertural surfaces (exclusive of pseudocolpi) reticulate (reticulum homobrochate) to bireticulate. Fig. 8b.

Daniel (1990b) recognized two species in this genus of North and Central America; and he reported P = 59–83 μm , E = 20–34 μm , and P:E = 1.2–3.4 in wet preparations. The exceptionally broad colpi are unique among New World Odontoneminae and are thus apomorphic for *Henrya* (see figures in Daniel 1990b, 1997). The basis for Gibson's (1974) description of pollen in *Henrya* as 4-porate remains unknown.

Holographis 15/16/16. Pollen euprolate to perprolate (P:E = 1.4–2.3), 3-colpate (or 3-colpoidate), P = 32–65 μm , E = 18–44 μm ; polar outline subtriangular to triangular; colpi (or colpoids) nearly as long as P, linear to \pm hourglass shaped or sometimes bifurcating near poles (arms of bifurcations sometimes fused with adjacent arms of other colpi near one or both poles), 1–8 μm wide at equator, surfaces psilate to \pm verrucate; interapertural surfaces psilate to verrucate to foveolate to rugulate. Fig. 2b, d.

Holographis is endemic to Mexico where it has radiated among deserts and other dry regions. Pollen of the genus (see figures in Daniel 1983b, 1986b, 1988c, 1997) resembles that of other Mexican Aphelandreae.

Hoverdenia 1/1/1. Pollen euprolate (P:E = 1.4–1.6), 3-colporate, 6-pseudocolpate, P = 67–75 μm , E = 43–48 μm ; polar outline triangular; colpi nearly as long as P, 12–14 μm wide at equator, barely exceeding (i.e., 1.5–1.8 times) diameter of ora in width, \pm elliptical, surfaces microverrucate to verrucate (often irregularly so with psilate regions); pseudocolpi 2 per mesocolpium, shorter than or as long as colpi, surfaces microverrucate to verrucate; interapertural surfaces (exclusive of pseudocolpi) psilate to foveolate, surfaces between colpi and adjacent pseudocolpi often \pm broken up or appearing degraded. Fig. 7c.

This unispecific genus is endemic to north-eastern Mexico. Its pollen is generally similar to that of other genera of Odontoneminae, except for the psilate to foveolate (vs. reticulate) interapertural surfaces and the regions between the colpi and the adjacent pseudocolpi which often appear eroded.

Hygrophila 1/2/80–100. Pollen spherical to prolate spheroidal (P:E = 1.0–1.1), P = 27–37 μm , E = 27–33 μm , 4-colporate, irregularly polypseudocolpate; polar outline subsquare; colpi fusiform, ca. 1/2–2/3 as long as P, 2–7 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate to verrucate; pseudocolpi 3–6 per mesocolpium, \pm unequal in length, mostly longer than colpi, surfaces microverrucate (often with psilate regions); exine between colpi divided into bands by pseudocolpi, bands rugulate. Figs. 4d, e; 11f.

This pantropical genus is represented in Mexico by a native species, *H. costata*, and an introduced species, *H. polysperma* (Roxb.) T. Anderson. Furness (1994) described pollen of 34 species of *Hygrophila* and recognized numerous pollen types and subtypes based on sculptural patterns, number and pattern of the pseudocolpi, and form of the endoapertures. Pollen of *H. costata* would appear to conform to her "*H. brasiliensis*-type," "subtype b." At least one species (*H. guianensis* Nees) studied by Furness (1994), the pollen of which conforms to this subtype, was treated by Daniel (1995c) as conspecific with *H. costata*. Furness (1994) noted that pollen of *Hygrophila* and *Brillantaisia* P. Beauv., an Old World genus of about 11 species with pollen nearly identical to that of *Hygrophila*, is unique in the Ruellieae. Elsewhere among Mexican Acanthaceae, 4-aperturate pol-

len has been found only in a few species of *Justicia*.

Hypoestes 1/1/70+. Pollen euprolate (P:E = 1.7–1.9), 3-colporate, 6-pseudocolpate, P = 44–50 μm , E = 25–26 μm ; polar outline triangular; colpi subfusiform, nearly as long as P, 1–2 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate; pseudocolpi 2 per mesocolpium, shorter than or nearly as long as colpi, surfaces microverrucate; interapertural surfaces (exclusive of pseudocolpi) reticulate (reticulum \pm homobrochate) to biretulate. Fig. 11i.

This paleotropical genus is represented in Mexico by the naturalized Malagasy endemic *H. phyllostachya*. Pollen of the species resembles that of native Mexican Odontoneminae as well as other Old World species of this genus (Balkwill and Norris 1985; Muller et al. 1989; Raj 1961).

Justicia 80/100+/ca. 600. Pollen 2–4-porate to 2–4-colporate, if 2-aperturate then globose-elliptic to globose-elongate (rarely with an equatorial constriction) (P:E in apertural view = 1.2–2.3; P:E in interapertural view = 1.3–4.1; longer E:shorter E = 1.1–2.0) and P = 23–87 μm and E (apertural view) = 16–42 μm and E (interapertural view) = 17–38 μm , if 3- or 4-aperturate then subprolate to perprolate (P:E = 1.2–2.7) and P = 27–90 μm and E = 18–54 μm ; polar outline elliptic to broadly elliptic to subrectangular (2-aperturate) or triangular to subcircular (3-aperturate) or subcircular to square (4-aperturate); trema area (see discussion below) present or absent, containing peninsulae and/or 2–6 rows of \pm discrete insulae, with an equal number of rows on each side of aperture(s) or (rarely) with more rows on one side than the other, insulae (2–) 4–10 (–14) per row, 1.3–8.0 μm in diameter, subcircular to elliptic to \pm irregular in shape, interinsular (and/or interpeninsular) surface of trema area subsilate to microverrucate to verrucate to verrucate-foveolate to microreticulate; colpi present (although often not prominent) or absent, usually fusiform, 2/5 as long to as long as P, 1.9–5.8 μm wide at equator, not to barely exceeding diameter of ora, rarely fusing at one or both poles (syncolpate), surfaces subsilate to microverrucate to verrucate to verrucate-rugulate; pseudocolpi absent or present, if present then 4 (in 2-aperturate grains) or 6 (in 3-aperturate grains) or 8 (in 4-aperturate grains), shorter

to longer than colpi in length, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces subpsilate to microverrucate to verrucate; interapertural surfaces (exclusive of trema areas, if present) microreticulate and studded with psilate echinae (i.e., *J. angustiflora*) to psilate-foveolate-microechinate (i.e., *J. medranoi*) to subpsilate to rugulate (with surfaces between rugulae verrucate in some *J. masiaca*) to reticulate (reticulum homobrochate to heterobrochate with lumina near poles smaller than lumina near equator) to bireticulate, lumina of reticulum psilate to verrucate to gemmate. Figs. 9a-i; 10a-i.

This is the largest genus of Acanthaceae with estimates of up to 600 species worldwide. Several genera with species in Mexico (e.g., *Chaetothylax* Nees, *Ixtlania* M. E. Jones, *Neohallia* Hemsl., *Siphonoglossa* Oerst., *Tabascinia* Baill.) have been included in *Justicia* recently, based, at least in part, on the pollen evidence (Daniel 1990a, 1995a; Graham 1988). Palynologically, *Justicia* is by far the most diverse genus of Mexican Acanthaceae (see figures in Acosta C. 1989; Acosta C. and Daniel 1993; Daniel 1990a, 1990c, 1993b, 1995a, 1995d, 1997; Henrickson and Hiriart 1988; Hilsenbeck 1990; Hilsenbeck and Marshall 1983; Meagher 1974; Ramamoorthy 1989; Wasshausen 1981; Wasshausen and Daniel 1995). Graham (1988) recognized 10 major types of pollen in the genus on a worldwide basis. Mexican species have been studied that resemble her types 1 and 3-9. Pollen resembling her type 2 might be present among the 12 species with 3-aperturate pollen; however, the distinguishing feature of this pollen type (sexine thickness) was not determined in the grains studied. At least two species have pollen that greatly resembles her type 10 except for the number of apertures (three in *J. longii* and four in *J. masiaca*). Pollen of several species does not conform to any of the types recognized by Graham (1988). For example, eight species studied have 4-aperturate pollen and none of the types recognized by Graham include grains with four apertures. Considering the characters used by Graham for recognizing pollen types, at least six could be recognized among these eight species.

Among the 80 species studied, eight have 4-aperturate pollen, 16 have 3-aperturate pollen, and 56 have 2-aperturate pollen. Among the latter, two species have pseudocolpi and 54 have

trema areas. For palynological descriptions of *Justicia*, trema areas are here defined as regions of thinner exine than found elsewhere on the grain, each containing a simple or compound aperture flanked by longitudinally arranged rows of more or less discrete insulae (which when not discrete from adjacent thicker portions of exine are termed peninsulae). The insulae vary greatly in size and number. They are usually arranged into \pm distinct longitudinal rows or, rarely, appear to be randomly disposed (e.g., *J. aurea*). A single row on each side of the aperture (i.e., two rows per trema area) is the most common pattern among Mexican species. The number of rows of insulae is not always consistent within a species. For example, in *J. candicans* the number of rows within a trema area varies from four to six. Sculpturing of the insulae resembles that found outside of the trema area. The trema areas rarely fuse across the poles (e.g., *J. valvata*, with connections between two of the four opposing pairs of trema areas) or join with adjacent trema areas near the equator (e.g., *J. jitotolana*, with sculpturing outside of the trema area restricted to the vicinity of the poles). Trema areas sometimes fuse near the poles to adjacent trema areas (e.g., *J. borraerae*, *J. tabascina*, *J. valvata*). Fusion of this type is reminiscent of fusion seen in pseudocolpi elsewhere in the family. In fact, pollen with pseudocolpi and pollen with trema areas appear to represent ends of a continuum rather than completely distinct pollen types (see also Meagher 1974 who concurs and Hilsenbeck 1990 who disagrees). The differences between them are a matter of degree and all intermediate stages between the extremes are evident among pollen of *Justicia* in Mexico. For example, colporate pollen with pseudocolpi is found in *J. ixtlania*; pollen in which the region of thick exine between the colpi and pseudocolpi is barely broken up into subdiscrete insulae is found in some *J. breviflora*, some *J. mirandae*, and in *J. sp.* (Cowan & Magaña 3138); and pollen with a well delimited trema area is found in most species (e.g., *J. candicans*). Sometimes, even within a species, a similar trend can be observed. Daniel (1995d) noted and illustrated variation in size and surface sculpturing in pollen of *J. masiaca* in which grains vary from having discrete, internally gemmate insulae in a trema area to having what appear to be fused insulae flanked by

pseudocolpi to lacking either a trema area or pseudocolpi.

Tricolporate, 6-pseudocolpate pollen similar to that generally encountered in subtribe Odononeminae is also found in *Justicia* of the Justiciinae (see also Henrickson and Hiriart 1988). Bremekamp's (1965) classification has the advantage of uniting these taxa within a single tribe, Justicieae. The relative distinction between pollen with pseudocolpi and pollen with trema areas is noted above. Although superficial pollen characters neither provide evidence for monophyly of *Justicia* nor distinguish the genus from other genera of Justicieae, the considerable diversity of palynological characters has been used for intrageneric classification (Graham 1988) and can be useful in species delimitation and recognition (e.g., Daniel 1995a, 1995d). Knowledge of pollen morphology in *Justicia* can reveal potential taxonomic problems as well. For example, Graham (1988) indicated that *J. liebmanii* V. A. W. Graham has type 9 pollen. Daniel (1995c) treated this species as conspecific with *J. spicigera*. Pollen of other specimens of *J. spicigera* have pollen resembling Graham's type 7, suggesting either taxonomic imprecision or the presence of different pollen types in a single taxon.

Some patterns of variation similar to those noted here are evident among southern African species of *Justicia* (Immelman 1987).

Lepidagathis 1/1/ca. 100. Pollen subprolate to euprolate (P:E = 1.2–1.8), 3-colporate, P = 21–36 μm , E = 16–20 μm ; polar outline subcircular to circular; colpi fusiform, ca. 2/3 to nearly as long as P, 2–3 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces verrucate; interapertural surfaces reticulate, reticulum heterobrochate, muri psilate, lumina verrucate to pilate, some of those flanking (but not immediately adjacent to) colpi larger than those at poles and near center of mesocolpia. Fig. 5i.

Lepidagathis is mostly paleotropical in distribution. Like its putative relatives *Lophostachys* and *Barleria*, its subfamilial position has never been stable. The sole Mexican species is sometimes treated in *Teliostachya* Nees (see Daniel 1995a for discussion of these genera).

Lophostachys 3/3/20. Pollen subprolate to euprolate (P:E = 1.2–1.4), 3-colporate, P = 64–81 μm , E = 46–60 μm ; polar outline subcircular; colpi \pm linear to fusiform, ca. 1/2–2/3 as long as

P, 2–6 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces psilate to verrucate; interapertural surfaces coarsely reticulate, reticulum heterobrochate, muri \pm psilate, lumina verrucate to gemmate to baculate to pilate, those near poles smallest and those flanking colpi largest. Fig. 5d, g.

Lophostachys is neotropical in distribution with three endemic species in Mexico. Daniel (1993a) illustrated the pollen of each. Among Mexican and Central American Acanthaceae pollen with similar surface sculpturing is known in *Ruellia* (Ruelliiinae), *Lepidagathis* (Lepidagathidinae), and *Barleria* (Barleriinae), each of which would be included in a different subtribe utilizing Bremekamp's (1965) classification. Benoist (1911) concluded that *Lophostachys* is not distinct from *Lepidagathis*. While his conclusion has not been generally accepted, the putative distinctions between these genera deserve additional study.

Louteridium 7/8/10. Pollen spherical (P:E = 1.0), pantoforate, diameter = 98–140 μm ; foramina more than 50, circular, 7–14 μm in diameter, surfaces microverrucate to microbaculate to micropilate; interapertural surfaces gemmate to baculate, regions between gemmae or baculae psilate to microverrucate to micropilate to finely rugulate. Figs. 3a; 11d.

This genus is restricted to Mexico and Central America. Its pollen is unique in the family and apomorphic for the Louterideae.

Mendoncia 2/2/50–60. Pollen spherical (P:E = 1.0), 5-colpate (see discussion), diameter 41–56 μm ; polar outline subpentagonal to subcircular; colpi narrowly linear, ca. 1/4–1/3 as long as pollen diameter, 1–2 μm wide at equator, surfaces irregularly verrucate, margins \pm protruding (liplike); interapertural surfaces finely rugulate, rugulae microverrucate and forming a dense, anastomosing patchwork over the surface. Figs. 1e, f; 11a.

Mendoncia occurs in the tropics of the New World, Africa, and Madagascar. Pollen of both Mexican species was figured by Daniel (1992). Pollen of the genus from regions outside of Mexico has been described as 3–6-colporate (Erdtman 1952; Muller et al. 1989; Raj 1961; Roubik and Moreno P. 1991; Scotland 1990a). Endoapertures (i.e., ora) were not observed in SEM preparations of Mexican species.

The taxonomic status of *Mendoncia* and its relatives is not resolved. The subfamily has been treated as a separate family (e.g., Bremekamp 1965; Cronquist 1981) and as a tribe within the Thunbergioideae (e.g., Takhtajan 1997). Scotland (1990a) noted that the tectal ornamentation and the morphology of the compound aperture (not described) are apparently unique features of *Mendoncia* pollen. As noted by Scotland (1990a), the uniqueness of its pollen does not help to resolve the taxonomic position of *Mendoncia*.

Mexacanthus 1/1/1. Pollen globose-oblong to globose-elongate (P:E = 1.6–1.8 in colpal view, 3.2–3.4 in intercolpal view; longer E:shorter E = 1.7–2.0), 2-colporate, 4-pseudocolpate, P = 48–66 μm , E = 27–39 μm (colpal view) and 20–23 (intercolpal view); polar outline subrectangular to elliptic; colpi fusiform, nearly as long as P, 7–8 μm wide at equator, barely exceeding diameter of ora, surfaces microverrucate to verrucate; pseudocolpi 2 per mesocolpium, shorter than or nearly as long as colpi, surfaces microverrucate to verrucate; interapertural surfaces (exclusive of pseudocolpi) reticulate, reticulum homobrochate. Fig. 8d.

Mexacanthus is endemic to western Mexico. Its Mexican relatives in the Odontoneminae (e.g., *Carlowrightia*, *Anisacanthus*, *Mirandea*) all have 3-colporate pollen. The secondarily bilateral (i.e., 2-colporate) pollen of *Mexacanthus* (see figures in Daniel 1981) would appear to be apomorphic for the genus in the subtribe.

Mirandea 4/4/4. Pollen spherical to perprolate (P:E = 1.0–2.0), 3-colporate, 6-pseudocolpate, P = 33–66 μm , E = 25–44 μm ; polar outline circular to triangular; colpi fusiform, nearly as long as P, 2–8 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate to verrucate; pseudocolpi 2 per mesocolpium, shorter than or as long as colpi, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces psilate to microverrucate; interapertural surfaces (exclusive of pseudocolpi) microverrucate-foveolate to bireticulate. Fig. 8h.

Mirandea is endemic to Mexico. Its pollen (see figures in Daniel 1978, 1986b) is similar to that of most other Mexican Odontoneminae. *Mirandea huastecensis* differs from *M. andradenia* and *M. sylvatica* by its pollen with interapertural surfaces microverrucate and foveolate (vs.

bireticulate). One collection of *M. grisea* (Daniel 852) has microverrucate sculpturing whereas another (Daniel 331) has foveolate-reticulate sculpturing.

Nelsonia 1/1/1+. Pollen euprolate (P:E = 1.6–1.9), 3-colpate, P = 34–39 μm , E = 18–21 μm ; polar outline subtriangular to triangular; colpi nearly as long as P, 1–2 μm wide at equator, narrowly linear, surfaces not seen; interapertural surfaces reticulate, reticulum \pm heterobrochate, larger lumina irregularly dispersed. Figs. 1i; 1lc.

The number of species recognizable in this pantropical genus is controversial (cf. Barker 1986; Hossain 1984). Scotland (1990a) described pollen of *Nelsonia* as 3-colporate; Muller, Schuller, Straka, and Friedrich (1989) and Erdtman (1952) described it as 3-colporoid (or 3-colporoidate); and Roubik and Moreno P. (1991) described it as 3- or 4-porate (although their figures reveal 3-colporate grains). Endoapertures (ora) were not seen in SEM preparations examined by me. Among Mexican Nelsonioideae, exine sculpturing of *Nelsonia* pollen is more like that of *Staurogyne* than *Elytraria*. Pollen of *Nelsonia* is intermediate in size between these other genera.

Odontonema 8/8/29. Pollen oblate spheroidal to spherical to euprolate (P:E = 0.9–1.8), 3(–4)-colporate, 6(–8)-pseudocolpate, P = 33–62 μm , E = 30–44 μm ; polar outline circular to subtriangular; colpi fusiform, nearly as long as P, 2–11 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces psilate to verrucate; pseudocolpi 2 per mesocolpium, shorter than or as long as colpi, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces psilate to verrucate; interapertural surfaces (exclusive of pseudocolpi) foveolate to rugulate to reticulate (reticulum homobrochate) to bireticulate. Fig. 8i.

Odontonema is entirely American in its distribution. Baum (1982) and Daniel (1995b) noted that pollen of most species of *Odontonema* (see figures in Daniel 1995b) resembles that of most other Odontoneminae. They also noted the exceptional pollen of *Odontonema cuspidatum* which differs from that of all other species in the genus by having four colpi and eight pseudocolpi.

Poikilacanthus 3/3/10+. Pollen spherical to euprolate (P:E = 1.0–1.4), 5 (–6?)-porate, P = 53–65 μm , E = 49–57 μm ; polar outline \pm pen-

tagonal (where seen); pores \pm circular, 6–7 μm in diameter, surfaces psilate to subverrucate; interapertural surfaces covered with subcircular to rectangular to polygonal insulae, insulae comprising gemmate regions enclosed by thick, psilate to foveolate muri, either discrete (except sometimes near poles) and \pm evenly distributed over surface or sharing common endwalls and arranged in loops and bands (loops enclosing a band), sometimes becoming irregularly reticulate with internal muri; surfaces between insulae (or between bands and/or loops) irregularly reticulate. Fig. 6e, f.

This genus is entirely American in distribution. Two distinct types of pollen (see figures in Daniel 1991b; Ramamoorthy 1989; Scotland 1992) are evident among Mexican species of the genus. *Poikilacanthus macranthus* has discrete insulae whereas *P. capitatus* and *P. novogalicianus* have similar "insulae" linked in loops and bands. The apertures of *Poikilacanthus* pollen might with equal justification be treated as compound (i.e., comprising a colpus and an os) in both pollen types. Scotland (1992) noted that pollen of *Poikilacanthus* is 6-aperturate. Pollen of two Mexican species was observed to be 5-aperturate. The number of apertures in pollen of *P. capitatus* could not be determined with certainty, but likely is six.

Pollen of *Poikilacanthus* has been considered to be unique in the family (Raj 1961). Because pollen characters have traditionally been weighted heavily in infrafamilial classification of the Acanthaceae, the tribal position of the genus has sometimes been unclear. Based on macromorphological characters, especially the presence of a rugula in the corolla, *Poikilacanthus* resembles genera of Bremekamp's Justiciinae. In fact, pollen characters appear to be the only consistent means of distinguishing *Poikilacanthus* from *Justicia*. Pollen like that of *Poikilacanthus* is not known among the diverse pollen types so far recorded for *Justicia* (Graham 1988; although see discussion of *J. masiaca* above under *Justicia*, the pollen of which shows some similarities in exine sculpturing to that of *Poikilacanthus*). Pollen somewhat similar to that of *Poikilacanthus macranthus* (i.e., with the surface covered by discrete insulae) is known in the unispecific American genus *Megaskepasma* Lindau (which appears to have six or more apertures). Studies of the latter genus that address its

relationship to the former are desirable. Based on macromorphological and, to a lesser extent, palynological lines of evidence, *Poikilacanthus* could be readily accommodated in the Justiciinae.

Pseuderanthemum 9/10–15/40–60. Pollen oblate spheroidal to euprolate (F:E = 0.9–1.7), 3-colporate, 6-pseudocolpate, P = 34–68 μm , E = 34–46 μm ; polar outline circular to subtriangular; colpi fusiform, nearly as long as P, 1–15 μm wide at equator, not to barely exceeding diameter of ora in width, sometimes fused at poles (i.e., 3-syncolporate), surfaces (subpsilate to) verrucate; pseudocolpi 2 per mesocolpium, shorter than or as long as colpi, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces (subpsilate to) verrucate; interapertural surfaces (exclusive of pseudocolpi) (rugulate to) reticulate, reticulum homobrochate, lumina sometimes containing one or more pilae. Fig. 7f.

Pseuderanthemum is a pantropical genus much in need of revision. Pollen of those Mexican species examined (see figures in Daniel 1993b) is typical of that generally found in other Mexican Odontoneminae.

Ruellia 35/ca. 65/ca. 250. Pollen spherical to subspheroidal (including at least oblate spheroidal and prolate spheroidal, see discussion below), 3-porate (as observed in eight species, see discussion), longest diameter 45–99 μm ; polar outline circular; pores 7–20 μm diameter, surfaces psilate to verrucate; interapertural surfaces coarsely reticulate, reticulum \pm homobrochate, muri sharply acute to rounded, psilate (to irregularly microverrucate to microechinate), sometimes incomplete or irregular (especially near pores), lumina psilate to verrucate to gemmate, verrucae or gemmae usually \pm evenly distributed, varying in number and size. Figs. 5a–c; 11h.

Species of *Ruellia* occur worldwide and the genus is the second largest among Mexican Acanthaceae. Considering the diverse vegetative and floral characteristics among Mexican *Ruellia*, pollen of Mexican species (see figures in Daniel 1990a, 1990d, 1993b, 1996, 1997; Ramamoorthy and Hornelas U. 1988) is remarkably uniform in general aspect. This uniformity is further evident on a worldwide basis (Furness and Grant 1996; Muller et al. 1989; Raj 1961). Most of the 31 species of *Ruellia* from Africa and Madagascar examined by Furness and Grant

(1996) have pollen greatly resembling that of Mexican taxa. They noted deviations from this basic pattern in two species that were 5-porate, three species that have a region around the three pores resembling a very short colpus, and two species with a clavate (vs. coarsely reticulate) surface. They further noted that each of the 31 Old World species studied has a unique combination of pollen characters. Most of the observed variation in pollen of Mexican species of *Ruellia* involves grain size, form of the muri, and size and sculpturing of the lumina. Further study of Mexican species of *Ruellia* will be necessary to determine whether their pollen provides a similar suite of diagnostic characters at the specific level.

The particular form and sculpturing of *Ruellia* pollen can make thorough analysis of the grains based solely on SEM preparations difficult. Because of their more or less spherical form and coarse reticulum (which often makes locating the apertures difficult), the polar axis and equatorial plane can be impossible to determine. These are discernible only when at least two apertures are in the field of view. In the limited number of grains where such was the case, the P:E varies from oblate spheroidal to prolate spheroidal. In some preparations, no apertures were observed. Thus, it could not be determined with certainty whether all Mexican species studied indeed have three apertures or whether they all lack regions adjacent to the apertures suggestive of colpi.

Furness and Grant (1996) noted correlations among species with large (92–117 μm) pollen and presumed moth and bat pollination. The Mexican species examined here were grouped into seven classes based on differences in floral size, shape, and color that are presumably related to pollination syndromes. Although Mexican species with flowers that would appear to fit into bat (Faegri and van der Pijl 1979) and hummingbird (Grant and Grant 1968) syndromes have the largest pollen (up to 99 μm diameter), there is sufficient overlap among all seven classes so as to suggest that making correlations between pollen size and pollinators among Mexican species would be premature at this time.

Among Mexican Acanthaceae, pollen of *Ruellia* most closely resembles that of *Barleria* (of Bremekamp's Ruellieae: Barleriinae). Similarities between pollen of these genera were also noted by Furness and Grant (1996). Pollen similar to that of *Ruellia* is also known elsewhere

among flowering plants (e.g. Geraniaceae, Scotland 1990b).

Sanchezia 2/2/ca. 60. Pollen globose-oblong (longer apertural axis:interapertural axis = 1.9), 2-colporate, polypseudocolpate, sculptural features of one face $\pm 90^\circ$ out of phase with those of opposite face, longer apertural axis 80–88 μm , shorter apertural axis 61–65 μm , interapertural axis 44 μm , apertural face elliptic in outline, interapertural face more narrowly elliptic in outline; colpi \pm linear, shorter than longer axis of and longer than shorter axis of apertural face, 1 μm wide near ora, surfaces microverrucate; pseudocolpi 12–14 per apertural face, of varying lengths (progressively larger away from colpi), longer ones fusing near periphery of grain, oriented in \pm same direction as colpi (i.e., \pm perpendicular to one another on opposite apertural faces), some appearing to encircle pollen in interapertural view, surfaces microverrucate to subverrucate; exine between colpi divided into bands by pseudocolpi, \pm prominently protruding (liplike) on both sides of colpi at ora, bands psilate with a single row of foveae down the center, longest axis of foveae 1–4 μm . Fig. 3d, e.

Several species of this neotropical genus are cultivated for ornament. One of them, *S. parvibracteata*, is possibly native or naturalized in southern Mexico (Daniel 1995c) and another, *S. speciosa* is cultivated and possibly naturalized. Pollen of *Sanchezia* occurring in Mexico, like that of other Trichanthereae, is "loxodicolporate" (see *Bravaisia*). Based on specimens examined, the longer apertural axis is longer in *Sanchezia* than in *Bravaisia* and the perforations in the bands of *Sanchezia* tend to be larger than those in *Bravaisia*. Vasanthy and Pocock (1986) noted gradations between radially symmetric and "rotationally symmetric" pollen in a different species of the genus (*S. lampra* Leonard & L. B. Sm.).

Schaueria 1/1/10–15. Pollen prolate spheroidal to subprolate (P:E = 1.1–1.3), 3-colporate, 6-pseudocolpate, P = 42–46 μm , E = 36–39 μm ; polar outline not seen; colpi fusiform, nearly as long as P, 10–13 μm wide at equator, barely exceeding diameter of ora in width, surfaces microverrucate to verrucate; pseudocolpi 2 per mesocolpium, shorter than or as long as colpi, sometimes fusing near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces microverrucate to verrucate; in-

terapertural surfaces (exclusive of pseudocolpi) reticulate (reticulum \pm homobrochate) to bireticulate, reticulum sometimes irregularly fragmented (sometimes into insulae) and surrounded by thin, verrucate regions. Fig. 7h.

This neotropical genus of 10 to 15 species occurs in Mexico, Guatemala, and South America. Its pollen (see figures in Daniel 1990a; Hilsenbeck and Marshall 1983) is generally like that of other Mexican Odontoneminae. Fragmentation of that portion of the mesocolpium between the pseudocolpi, as seen in pollen from several collections, has not been observed in other Mexican Odontoneminae. Although not observed in *Schaueria*, similar fragmentation in that portion of the mesocolpium between the colpus and the adjacent pseudocolpi would result in pollen similar to that found in certain species of *Justicia*.

Spathacanthus 2/2/3. Pollen prolate spheroidal to euprolate, (P:E = 1.1–1.5), 3 (–4)-colporate, 6 (–8)-pseudocolpate, P = 39–64 μ m long, E = 28–43 μ m; polar outline subtriangular to subcircular (to square); colpi fusiform, ca. 1/2 to nearly as long as P, 10–15 μ m wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate to verrucate; pseudocolpi 2 per mesocolpium, as long as or longer than colpi, sometimes fused near one or both poles thereby forming pseudocolpal arcs or ellipses in mesocolpia, surfaces subpsilate to microverrucate; interapertural surfaces (exclusive of pseudocolpi) foveolate to fossulate to verrucate to rugulate. Fig. 8g.

Spathacanthus occurs only in southern Mexico and Central America. Its pollen is generally like that of most other Mexican Odontoneminae (see *Chalarothyrsus*), except that the interapertural surfaces are not conspicuously reticulate. One collection of *S. parviflorus* (*Skutch 961*) has pollen with four colpi whereas another (*Matuda 1696*) has some grains with three colpi and others with four. Variation of aperture number within a species was encountered elsewhere among Mexican Acanthaceae only in *Stenandrium dulce*. Figure 8 shows pollen of a Costa Rican species, *S. hoffmannii* Lindau, that resembles pollen of Mexican species.

Staurogyne 1/1/80–140. Pollen (see discussion) perprolate (P:E = 2.2–2.3) or suboblate to spherical (P:E = 0.8–1.0), 3-colporate or 3-colpate to 3-colporoidate, P = 28–30 μ m and E = 12–13 μ m or P = 15–17 μ m and E = 17–18 μ m;

polar outline subcircular to subtriangular; colpi narrowly linear or fusiform, nearly as long as P, 1 μ m or 3–4 μ m wide at equator, surfaces verrucate (where seen); interapertural surfaces reticulate, reticulum \pm homobrochate. Fig. 1j.

Staurogyne is a pantropical genus with a majority of species occurring in southeastern Asia. Pollen of the sole species known from North and Central America, *S. agrestis*, is described above. It appears to be similar to that reported elsewhere in the genus (Raj 1961; Scotland 1990a). Pollen of *Lott et al. 3396* (see figure in Daniel and Lott 1993) is spherical to oblate and conspicuously colporate whereas pollen of *Lott et al. 3226* is perprolate and either colpate or colporoidate (i.e., endoapertures, if present, were not seen). Interestingly, these two collections were both made in the same general region of coastal Jalisco. Scotland (1990a) indicated that pollen of species he studied were 3-colporate but often with the endoapertures indistinct. Among Mexican Nelsonioideae, the interapertural exine sculpturing of pollen of *Staurogyne* is more like that of *Nelsonia* than *Elytraria*. Based on the samples examined, *S. agrestis* has smaller pollen than other Mexican species of the subfamily.

Stenandrium 9/9/ca. 65. Pollen (except some *S. dulce*, see below) euprolate to perprolate (P:E = 1.4–2.2), sometimes slightly hourglass shaped due to a slight equatorial constriction, 3-colpate, P = 33–55 μ m, E = 18–29 μ m; polar outline circular to triangular; colpi linear to hourglass shaped, nearly as long as P, 1–6 μ m wide at equator, sometimes bifurcating near poles (arms of bifurcations sometimes fusing with adjacent arms of other colpi near one or both poles), surfaces psilate to microverrucate to verrucate to subrugulate; interapertural surfaces psilate to foveolate to fossulate to rugulate. Pollen of some individuals of *S. dulce*: spherical (P:E = ca. 1.0), 33–42 μ m in diameter, inaperturate, surfaces verrucate to gemmate, verrucae and gemmae usually of two distinct sizes. Fig. 2e–i.

Stenandrium occurs in Africa, Madagascar, and the New World. Palacios C. and Quiroz G. (1994) described and figured pollen of seven of the Mexican species. The observations above include information from the two Mexican species, *S. subcordatum* and *S. verticillatum*, not examined by them. In general, my observations agree with those of Palacios C. and Quiroz G. (1994); however, I could not substantiate their

descriptions of *S. dulce* as trichotomocolpate, *S. manchonense* as dicolpate, and *S. pilosulum* as dicolpate to tricolpate. (In fact, some confusion exists in their paper concerning the number of apertures in the latter two taxa, cf. the table vs. the text.) Furness (1993) recognized four pollen types among Old World species of *Stenandrium* studied by her. Pollen of most Mexican species more closely resembles her pollen type I which is only found in taxa from Madagascar. The unusual inaperturate pollen of some individuals of *S. dulce* has been reported for the species from throughout its wide range (Ariza Espinar and Ferrucci 1982; Furness 1993; Heusser 1971; Marticorena P. 1968). I have also examined pollen of this species from Florida (*Standley 71*), Argentina (*Renvoize 3428*), and Bolivia (*Davidson 3746*); pollen from each of these collections resembles that described above for individuals with inaperturate grains. Lindau (1895) divided *Stenandrium* into two sections based solely on these two different types of pollen.

Interestingly, among the Mexican collections of *S. dulce* studied, both 3-colpate and inaperturate pollen was encountered (but never both types from the same collection). Three collections (*Breedlove & Almeda 45287*, *Chiang et al. 8198*, and *Hinton 6086*) have the euprolate to perprolate, 3-colpate pollen resembling other Mexican species of the genus whereas three other collections (*Angeles 2*, *Hernández M. 5995*, and *Padilla 8*) have the spherical, inaperturate grains. Further study is needed to determine whether the presence of two pollen types among Mexican collections treated as *S. dulce* is indicative of inadequate taxonomic refinement or a remarkable palynological dimorphism within a single species. The sections of *Stenandrium* as delimited by Lindau (1895) also would appear to require some modification. Pollen similar to the spherical, inaperturate grains sometimes found in *S. dulce* also is known in the South American species (and apparent close relatives of *S. dulce*) *S. trinerve* Nees (Petriella 1968; Raj 1961) and *S. pohlii* Nees (Raj 1961). In fact, Ezcurra (1993) utilized this pollen difference in her key to species and included one variant of *S. trinerve* within *S. dulce*.

Furness (1993) noted the palynological similarity between *Stenandrium* and *Crossandra* Salisb., an Old World genus of the Acantheae. Among New World Aphelandreae, pollen of

Stenandrium resembles that of *Holographis* and *Aphelandra*, the only other representatives of this tribe in Mexico. Even some of the same tendencies observed in *Stenandrium* (e.g., colpi bifurcating near poles) are to be found in both of these other genera.

Stenostephanus 15/15/ca. 65. Pollen globose-elliptic to globose-elongate (longer E:shorter E = 1.0–2.8), 2-porate, diameter in apertural view = 31–56 μm , E in interapertural view = 16–48 μm ; outline in apertural view circular to subcircular, outline in interapertural view narrowly elliptic to broadly elliptic to circular; pores 3–9 μm diameter, verrucate to gemmate to echinate, each pore surrounded by a circular region 17–47 μm in diameter, surface of circular regions subsilate to microverrucate to microrugulate and also gemmate to baculate to echinate, the two circular regions separated by a peripheral band 2–15 μm wide, surface of peripheral band psilate to verrucate to rugulate (and sometimes with a central row of gemmae to baculae to echinae). Fig. 6a–d.

This neotropical genus is most diverse in the northern Andes of South America. Two distinctive forms of pollen (see additional figures in Daniel 1995a) were encountered among the Mexican species of *Stenostephanus*: globose-elongate (i.e., longer E:shorter E = 2.0–2.8 and the interapertural outline narrowly elliptic; 6 spp.) and globose-elliptic (i.e., longer E:shorter E = 1.0–1.5 and the interapertural outline broadly elliptic to circular; 9 spp.). Whether this difference can be correlated with other characters and thus be useful in the infrageneric classification of *Stenostephanus* is currently under study. Considerable variation in the width and sculpturing of the peripheral band was noted among species.

Stenostephanus and its relatives were included by Bremekamp (1965) in subtribe Isoglossinae (as "Rhytiglossinae") of tribe Justiciaeae. Macro-morphologically, *Stenostephanus* is similar to the African genera *Oreacanthus* Benth. and *Brachystephanus* Nees. Pollen similar to both types found in *Stenostephanus* is also found in *Brachystephanus* and the globose-elongate pollen of *Stenostephanus* is characteristic of *Oreacanthus*. *Brachystephanus* appears to encompass considerably more diversity in its pollen than seen among Mexican *Stenostephanus* (Figueiredo and Keith-Lucas 1996). The taxonomic relationships of *Stenostephanus* and its New World relatives with similar pollen (e.g., *Razisea*

Oerst.) to various other Old World genera with superficially similar pollen (e.g., *Conocalyx* Benoist, *Forcipella* Baill., *Isoglossa* Oerst., *Leandriella* Benoist, and *Sphacanthus* Benoist, as depicted by Muller et al. 1989) warrant further study.

Tetramerium 20/21/28. Pollen subprolate to perprolate (P:E = 1.3–3.0), 3-colporate, 6-pseudocolpate, P = 29–79 (–120) μm , E = 14–33 (–41) μm ; polar outline circular to triangular; colpi fusiform, nearly to as long as P, 1–5 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate to verrucate to subgemmate; pseudocolpi 2 per mesocolpium, nearly to as long as colpi, often fusing near poles thereby forming pseudocolpal ellipses in mesocolpia, surfaces psilate to microverrucate; interapertural surfaces (exclusive of pseudocolpi) (rugulate to) reticulate (reticulum homobrochate) to biretulate. Fig. 7b.

Most of the species in this American genus occur in Mexico. Except for considerable variation in size, pollen morphology is highly consistent throughout the genus and resembles that of other Mexican Odontoneminae (see figures in Daniel 1986a, 1997).

Thunbergia 4/5/100–200. Pollen spherical to subprolate (P:E = 1.0–1.2), spiraperturate (= spiro-treme), P = 49–74 μm , E = 45–66 μm ; polar outline circular; apertures one or apparently several per grain, dividing grain into horizontal bands in equatorial view, 1–4 μm wide, surfaces psilate to scabrate to verrucate; interapertural surfaces subpsilate (e.g., *T. alata*) to verrucate (e.g., *T. erecta*) to rugulate with a single line of prominent verrucae to baculae (e.g., *T. fragrans*). Fig. 1a–d.

At least five species of this paleotropical genus are cultivated in Mexico and at least two of those are naturalized as well. The taxonomic position of the Thunbergioideae (i.e., whether treated as a subfamily of Acanthaceae or a separate family) remains to be resolved. Pollen of species studied here resembles that described from other collections and other species of *Thunbergia* (Bremekamp 1955; Erdtman 1952; Natarajan 1957; Raj 1961, 1973; Roubik and Moreno P. 1991; Valsaladevi and Mathew 1989). Linear-spiral apertures (or their derivatives), as seen in pollen of *Thunbergia*, are synapomorphic for *Pseudocalyx* Radlk. and *Thunbergia* (but not *Meyenia* Nees) in the Thunbergioideae among Acanthaceae.

Spiraperturate pollen is known outside the Acanthaceae in genera representing several families (Sheta and Brack-Hanes 1984).

Yeatesia 2/2/3. Pollen subprolate to euprolate (P:E = 1.3–1.4), 3-colporate, 6-pseudocolpate to 6-pseudocolpoidate, P = 47–51 μm , E = 36–42 μm ; polar outline subtriangular; colpi fusiform, ca. 1/2 to nearly as long as P, 3–8 μm wide at equator, not to barely exceeding diameter of ora in width, surfaces microverrucate to verrucate to gemmate; pseudocolpi 2 per mesocolpium, distinct to subdistinct, mostly shorter than colpi, surfaces microverrucate to verrucate; interapertural surfaces (exclusive of pseudocolpi) reticulate (reticulum homobrochate) to biretulate, muri psilate or microverrucate. Fig. 7j.

Yeatesia is endemic to North America. Its pollen (see figures in Hilsenbeck 1989) is similar to that of other genera of Odontoneminae. Pollen of *Y. platystegia* differs from that of *Y. mabryi* by its reticulate (vs. biretulate) sculpturing with microverrucate (vs. psilate) muri and poorly developed (vs. well developed) pseudocolpi. Acetolyzed pollen of *Y. platystegia* (Hilsenbeck 1989) shows even less distinct pseudocolpi and poorly developed colpi. In all other features, my observations agree with photographs of *Yeatesia* pollen provided by Hilsenbeck (1989). The only other species of the genus, *Y. viridiflora* (Nees) Small, which is endemic to the United States, has pollen similar to that of *Y. platystegia* but with even less distinct pseudocolpi. Species of the genus appear to exhibit decreasing development of the pseudocolpi in a northward geographic direction.

SUMMARY AND CONCLUSIONS

The tremendous diversity of pollen morphology in the family is amply reflected among the genera of Mexican Acanthaceae. Palynological diversity is evident in grain size (P varies from 21 to 140 μm) and shape (oblate to prolate); aperture number (two to more than fifty), shape (colpi or pores), structure (simple or compound), and position (equatorial to global); and exine sculpturing (e.g., psilate to fossulate to reticulate to gemmate). The diversity of acanthaceous pollen in Brazil, India, and Madagascar would likely equal, or even surpass, that so far documented from Mexico if sufficiently detailed palynological studies of those countries, each also rich in

Acanthaceae, were available. In the genera studied here, pollen diversity is generally taxonomic rather than geographic in nature. For example, pollen of genera comprising both Mexican and Old World species (e.g., *Dicliptera*, *Dyschoriste*, *Hygrophila*, *Justicia*, *Ruellia*, and *Stenandrium*) is decidedly consistent within each genus.

The morphological attributes considered in this study provide useful systematic data primarily at the generic and suprageneric levels. Most Mexican genera consist of species with pollen that is relatively homogeneous, especially in characteristics of the apertures. Therefore, pollen is often useful in the characterization of genera (e.g., *Henrya*, *Louteridium*, *Ruellia*, *Poikilacanthus*). Although most genera have relatively homogeneous pollen, others show heterogeneity among species to a greater (e.g., *Justicia*) or lesser (e.g., *Odontonema*) extent. The presence of one species with unusual pollen in an otherwise palynologically homogeneous genus was encountered several times (e.g., *Stenandrium*, *Odontonema*). One limitation of broad, superficial surveys of pollen is that this latter type of variation, which can be crucial in determining character polarity for phylogenetic reconstruction, is often missed. The presence of individual species with unique pollen within a genus emphasizes the need to study pollen of all species of genera. A similar argument might be applied to species where extensive sampling of individuals should likewise be undertaken. For the most part in this study few samples from any single species were studied; therefore, variation at the species level usually was not ascertained. In most instances where more than one sample of a species was studied, little variation was observed. In some cases, however, where significant variation was seen, more extensive sampling was undertaken. Further studies will be needed to better understand the significance of palynological variation in species such as *Aphanosperma sinaloensis*, *Spathacanthus parviflorus*, and *Stenandrium dulce*.

Other than the lack of extensive sampling within a species, a significant deficiency of this investigation is the lack of observations on pollen structure. Studies of the internal structure of the exine should help to resolve whether pollen of *Mendoncia*, *Elytraria*, and *Nelsonia* in Mexico have endoapertures as reported previously but which were not evident in the samples I ob-

served. Also, the sculpturing patterns of interapertural surfaces of unacetolyzed pollen likely differs from that of acetolyzed grains in some instances (e.g., some surfaces here characterized as reticulate might be revealed to be bireticulate in acetolyzed pollen).

Obvious correlations of pollen form to known pollinators were not established by my observations (see *Ruellia*). In some instances a positive correlation between pollen size and flower size was noted (e.g., *Braviasia* and *Justicia masiaca*, cf. Daniel 1995d). Unusual features of pollen grains sometimes could be associated with taxonomy, but other times could not. In several genera, the colpi often contain an elevated ridge surrounding the ora and tapering toward the poles. The ridge is usually covered with larger sculptural elements than the surrounding colp surface. This colp ridge is particularly evident in pollen of *Gypsacanthus*, *Mexacanthus*, and *Schaueria*; but it was also observed in some pollen of *Anisacanthus*, *Carlowrightia*, *Tetramerium*, and *Yeatesia*. All of these genera are in subtribe Odontoneminae. Another unusual palynological feature, protruding (liplike) exine on each side of the ora, was seen in pollen of the taxonomically unrelated genera *Dyschoriste* and *Braviasia*. A similar and very rare feature present in even more distantly related genera is the tripartite, aperturelike indentation at the poles in some individuals of *Aphanosperma* and in some species of *Aphelandra*. These regions of thin exine are probably best considered as pseudoapertures, and like pseudocolpi, possibly have a harmomegathic function.

Because pollen characters have been routinely used in suprageneric classification of Acanthaceae, it is not surprising that there tend to be good correlations between pollen form and systematic classification. As noted in the generic discussions above, several of the suprageneric taxa listed in Table 1 are supported by palynological as well as macromorphological characters. For example, each of the Mendoncioideae, Trichanthereae, and Louteridieae has a unique pollen type in the family. Bremekamp's (1965) classification, although incomplete, offers some advantages with respect to that of Lindau (1895). Daniel, Chuang, and Baker (1990) noted that it incorporated some related taxa, previously treated in different tribes, into the same subtribe. It also unites within the Jus-

ticieae two subtribes (Justiciinae and Odon-toneminae) that share a common pollen type (i.e., 3-colporate, 6-pseudocolpate). *Poikilacanthus*, treated by Bremekamp (1965) as being of uncertain position in the Justicieae, could be accommodated in subtribe Justiciinae. The unusual pollen of *Stenostephanus* and its relatives in subtribe Isoglossinae suggest that it may not be as closely related to the other subtribes in the Justicieae as they are to one another. Bremekamp's classification would also appear to have some disadvantages with respect to that of Lindau. For example, Lindau (1895) included *Barleria*, *Lepidagathis*, and *Lophostachys* within the same tribe (Barlerieae) whereas Bremekamp (1965) removed *Lepidagathis* to a different tribe. The palynological similarities of these genera, combined with certain macromorphological characteristics, suggest that they might be better treated in the same tribe. In fact, the generic distinctions between the latter two genera have been questioned (Benoist 1911). Also, Bremekamp's subtribe Odon-toneminae brings together many Mexican genera with similar pollen (i.e., 3-colporate, 6-pseudocolpate or pollen derived from this type). Macromorphological and cytological evidence, however, suggests at least three groupings among the genera here included in the subtribe (Daniel and Chuang 1993).

Because pollen of Acanthaceae is diverse and because it is often rather homogeneous within a genus, palynological characters will continue to be used both in the characterization of genera and in assessing their phylogenetic relationships. Despite more than a century of describing pollen of Acanthaceae, many genera remain palynologically inadequately diagnosed and the pollen of most species has yet to be described. Descriptions of pollen, based on original observations, in monographic and floristic studies of Acanthaceae are highly desirable.

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APPENDIX

Taxa and collections from which pollen was examined. Collections denoted with and asterisk (*) were made outside of Mexico. Taxa for which combinations have not been made in the genus in which they are included here are listed at the end of the genus (i.e., *Justicia* and *Stenostephanus*).

Anisacanthus Nees

- A. andersonii* T. F. Daniel: *McCarten & Bittman* 2690.
A. junceus (Torr.) Hemsl.: *Daniel* 479.
A. linearis (Hagen) Henr. & E. J. Lott: *Daniel* 538.
A. puberulus (Torr.) Henr. & E. J. Lott: *Johnston et al.* 10571.
A. punilis (Dietr.) Nees: *Lott & Magallanes* 313.
A. quadrifidus (Vahl) Nees: *Daniel* 256, *Daniel* 1260.
A. thurberi (Torr.) A. Gray: *Daniel* 118*.

Aphanosperma T. F. Daniel

- A. sinaloensis* (Leonard & Gentry) T. F. Daniel: *Daniel* 4070, *Daniel et al.* 6866, *Gentry* 7111, *Van Devender et al.* 93-1494.

Aphelandra R. Br.

- A. aurantiaca* (Scheidw.) Lindl.: *Breedlove* 71287, *Shapiro* 262.
A. gigantiflora Lindau: *Breedlove* 70900, *Standley* 19771.
A. guerrerensis Washh.: *Daniel* 5376, *Hinton* 11199, *Reko* 6051.
A. heydeana Donn. Sm.: *Breedlove* 65803.
A. hintonii Washh.: *Hinton* 16049.
A. lineariloba Leonard: *Daniel s.n.cv.*
A. madrensis Lindau: *Daniel* 5276, *Langlassé* 806, *Lott* 865.
A. scabra (Vahl) Sm.: *Daniel* 5328.
A. schiedeana Schldl. & Cham.: *Ventura A.* 12241.
A. speciosa Brandege: *Croat* 40837.
A. verticillata Nees ex Hemsl.: *Daniel et al.* 3295, *Hinton* 13486, *Moore* 5503.
A. wendtii T. F. Daniel: *Breedlove* 22121, *Daniel & Wendt* 5813.
A. sp.: *A. Delgado S.* 635.

Barleria L.

- B. oenotheroides* Dum. Cours.: *Breedlove & Daniel* 71185, *Daniel* 5327, *Daniel et al.* 8412.

Blechum P. Browne

- B. grandiflorum* Oerst.: *Breedlove* 50544.
B. pyramidatum (Lam.) Urb.: *Daniel* 2057, *Daniel et al.* 5454*.

Bravaisia DC.

- B. berlandieriana* (Nees) T. F. Daniel: *Cabrera & Ibara* 1149.
B. grandiflora Donn. Sm.: *Daniel & Bartholomew* 4998.
B. integerrima (Spreng.) Standl.: *Daniel* 2144.

Carlowrightia A. Gray

- C. albiflora* T. F. Daniel: *Daniel* 276.
C. arizonica A. Gray: *Daniel* 173*, *Daniel* 203*, *Daniel* 983, *Daniel* 1157, *Daniel et al.* 6845.
C. fuertensis T. F. Daniel: *Rose et al.* 13585.
C. hapalocarpa B. L. Rob. & Greenm.: *Daniel* 854.
C. henricksonii T. F. Daniel: *Johnston & Crutchfield* 5357.
C. hintonii T. F. Daniel: *Hinton* 11326.
C. huicholiana T. F. Daniel: *Bauml & Voss* 1896.
C. lesueurii Henr. & T. F. Daniel: *LeSueur* 1254.
C. linearifolia (Torr.) A. Gray: *Daniel* 565.
C. mcvaughii T. F. Daniel: *Feddema* 173.
C. mexicana Henr. & T. F. Daniel: *Henrickson & Lee* 16013.
C. myriantha (Standl.) Standl.: *Gaumer* 1102.
C. neesiana (Schauer ex Nees) T. F. Daniel: *Daniel* 417.
C. ovata A. Gray: *Pringle* 695.
C. parviflora (Buckley) Washh.: *Daniel* 899.
C. parvifolia Brandege: *Daniel* 547.
C. pectinata Brandege: *Daniel* 936, *Daniel* 6846.
C. pringlei B.L. Rob. & Greenm.: *Daniel* 1291.
C. purpurea T. F. Daniel: *Daniel* 351.
C. serpyllifolia A. Gray: *Daniel* 221, *Daniel* 653.
C. texana Henr. & T. F. Daniel: *Daniel* 108*.
C. torreyana Washh.: *Daniel* 97*.
C. trichocarpa T. F. Daniel: *Daniel* 260.

Chalarothyrsus Lindau

- C. amplexicaulis* Lindau: *Daniel & Bartholomew* 4842.

Chileroanthemum Oerst.

- C. lottae* T. F. Daniel: *Paray* 2857, *Paray* 2858.
C. pyramidatum (Lindau) T. F. Daniel: *Breedlove* 27655, *Torres C.* 121.
C. trifidum Oerst.: *Rosas R.* 1020.

Dicliptera Juss.

- D. acuminata* (Ruiz & Pav.) Juss.: *Ventura A.* 15758.
D. anomala Leonard: *Hernández G.* 840.
D. haenkeana Nees: *Daniel* 5290.
D. inequalis Greenm.: *Daniel & Bartholomew* 4860.
D. inutilis Leonard: *Daniel & Bartholomew* 4877.
D. nervata Greenm.: *Daniel* 4009.
D. peduncularis Nees: *Daniel* 1262.
D. resupinata (Vahl) Juss.: *Daniel et al.* 1947, *Daniel et al.* 2489, *Daniel et al.* 6865, *Ross et al.* 2061.
D. sciadephora Donn. Sm.: *Daniel & Bartholomew* 5026.
D. sexangularis (L.) Juss.: *Palmer* 93.
D. sumichrasti Lindau: *Tenorio L. et al.* 5834.
D. thlaspioides Nees: *Breedlove* 35983, *Daniel* 1292.
D. unguiculata Nees: *Camp* 2430.

Dyschoriste Nees

- D. angustifolia* (Hemsl.) Kuntze: *Daniel* 5310.
D. decumbens (A. Gray) Kuntze: *Jones* 24437.
D. capitata (Oerst.) Kuntze: *Breedlove* 26151.
D. hirsutissima (Nees) Kuntze: *Daniel & Butterwick* 3260.
D. mcvaughii T. F. Daniel: *Daniel & Bartholomew* 4828, *McVaugh* 12187.
D. microphylla (Cav.) Kuntze: *Ventura A.* 5714.
D. novogaliciana T. F. Daniel: *Daniel* 2051, *Daniel & Bartholomew* 4779.
D. ovata (Cav.) Kuntze: *Breedlove & Strother* 46563.
D. pringlei Greenm.: *Villa C. & Chávez L.* 755.
D. purpusii Kobuski: *Breedlove* 69496.
D. quadrangularis (Oerst.) Kuntze: *Breedlove & Anderson* 63705.
D. saltuensis Fernald: *Daniel & Bartholomew* 4848.
D. schiedeana (Nees) Kuntze: *Orcutt* 1654.
D. xylopoda Kobuski: *Wilbur & Wilbur* 2137.
D. sp.: *Daniel & Bartholomew* 4860.5.

Elytraria Michx.

- E. bromoides* Oerst.: *Daniel* 303, *Daniel & Baker* 3683.
E. imbricata (Vahl) Pers.: *Daniel & Butterwick* 3259gh, *Porter* 297.
E. macrophylla Leonard: *Carranza* 2397, *Dressler* 2619.
E. mexicana Fryxell & S. D. Koch: *Daniel & Butterwick* 3263gh.

Gypsacanthus E. J. Lott, V. Jaram. & Rzed.

- G. nelsonii* E. J. Lott, V. Jaram. & Rzed.: *Trejo V.* 390.

Henrya Nees ex Benth.

- H. insularis* Nees ex Benth.: *Daniel* 2116, *Daniel & Bartholomew* 4731, *Daniel & Bartholomew* 4822, *Sanders et al.* 2613gh.
H. tuberculosperra T. F. Daniel: *Daniel & Bartholomew* 4868.

Holographis Nees

- H. anisophylla* T. F. Daniel: *Lott* 2359.
H. argyrea (Lundell) T. F. Daniel: *Daniel* 1242.
H. cuicatlanensis Salinas T.: *Salinas T.* 5274, *Salinas T.* 6104, *Salinas T. et al.* 4779.
H. ehrenbergiana Nees: *González* 3581.
H. ilicifolia Brandege: *Daniel* 659.
H. leticiana T. F. Daniel: *Torres C.* 637.
H. medusae T. F. Daniel: *Daniel & Bartholomew* 4918.
H. pallida Leonard & Gentry: *Gentry* 7022.
H. parayana Miranda: *Daniel* 6203.
H. peloria (Leonard) T. F. Daniel: *Télez V. & Miller* 10628.
H. pueblensis T. F. Daniel: *Daniel & Baker* 3771, *Purpus* 3346.
H. tamaulipica T. F. Daniel: *Woodruff et al.* 166.
H. tolantongensis T. F. Daniel: *Hernández M. & Tenorio L.* 6948.
H. virgata (Harv. ex Benth. & Hook.) T. F. Daniel: *Breedlove* 60981, *Carter & Ferris* 3819, *Carter & Sharsmith* 4215, *Carter et al.* 5724, *Moran* 3928.
H. websteri T. F. Daniel: *Webster & Lynch* 17724.

Hoverdenia Nees

- H. speciosa* Nees: *Daniel & Baker* 3739, *Rzedowski* 36934.

Hygrophila R. Br.

H. costata Nees: Daniel & Butterwick 5884*,
Daniel et al. 4316*, Daniel et al. 8163cv*,
Wendt 3109.

Hypoestes Sol. ex R. Br.

H. phyllostachya Baker: Breedlove & Daniel
70764, Daniel s.n.*.

Justicia L.

(including taxa for which nomenclatural combinations have not been published)

J. adenothyrsa (Lindau) T. F. Daniel: Daniel & Bartholomew 4981.

J. alopecuroidea T. F. Daniel: Daniel & Bartholomew 4980.

J. americana (L.) Vahl: Lieb & Roessling 645*.

J. anagallis (Nees) Lindau: Ventura A. 7071.

J. angustiflora D. N. Gibson: Reyes 1255.

J. aurea Schtdl.: Breedlove 29496.

J. austrocapensis T. F. Daniel: Moran 7373.

J. bartlettii (Leonard) D. N. Gibson: Breedlove & Almeda 57832.

J. borraerae (Hemsl.) T. F. Daniel: Breedlove 35290.

J. brandegeana Wssh. & L. B. Sm.: Daniel 291.

J. breedlovei T. F. Daniel: Breedlove 56242.

J. breviflora (Nees) Rusby: Breedlove 50689,
Breedlove 68976, Daniel & Bartholomew
5010, Lott & Magallanes 1860.

J. californica (Benth.) D. N. Gibson: Daniel et al. 1542.

J. campechiana Standl. ex Lundell: Cabrera C. 9938, Miranda 5860, Miranda 6839.

J. canbyi Greenm.: Garcia M. & Ramos 2909.

J. candelariae (Oerst.) Leonard: Breedlove 67008, Skutch 2009*.

J. candicans (Nees) L. D. Benson: Daniel 8355, Moran 18787.

J. carthagenensis Jacq.: Breedlove 7718, Breedlove 34000.

J. caudata A. Gray: Breedlove & Daniel 70945.

J. chol T. F. Daniel: Cowan & Magaña 3138.

J. clinopodium A. Gray ex Greenm.: Daniel et al. 5873.

J. colorifera V. A. W. Graham: Breedlove 50321.

J. comata (L.) Lam.: Breedlove 38648.

J. decurvata Hilsenb.: Torrecillas 217.

J. eburnea D. N. Gibson: Tún O. 1134.

J. fimbriata (Nees) V. A. W. Graham: Breedlove 49679, Daniel & Bartholomew 4992.

J. fulvicoma Schtdl. & Cham.: Daniel & Baker 3637.

J. gonzalezii Henr. & Hiriart: Daniel & Baker 3779.

J. herpetacanthoides Leonard: Breedlove & Daniel 71004.

J. hians (Brandegge) Brandegge: Carter et al. 4164.

J. inaequalis Benth.: Matuda 3990.

J. insolita Brandegge: Carter 5711, León de la Luz 2334.

J. ixtlania T. F. Daniel: Daniel 2070.

J. jitotolana T. F. Daniel: Thorne & Lathrop 41662, Zwill 631.

J. kanal T. F. Daniel: Breedlove & Bourell 68262.

J. linearis B.L. Rob. & Greenm.: Daniel & Baker 3719.

J. lindeniana (Nees) J. F. Macbr.: Breedlove 49908.

J. longii Hilsenb.: Butterwick & Hillyard 7384*, Kearney & Peebles 14969*.

J. macrantha Benth.: MacDougall s.n..

J. madrensis T. F. Daniel: Breedlove 38656.

J. masiaca T. F. Daniel: Daniel et al. 2546, Van Devender & Sanders 92-1058, Van Devender et al. 93-827, White 3590.

J. medranoi Henr. & Hiriart: Daniel & Baker 3742.

J. mirandae T. F. Daniel: Breedlove 50163.

J. multicaulis Donn. Sm.: Breedlove 49946.

J. nevlingii Wssh. & T. F. Daniel: Dorantes 2799, Marcks & Marcks 913, Vazquez et al. 411.

J. palmeri Rose: Carter 5442.

J. pectoralis Jacq.: Breedlove 48559.

J. phlebodes Leonard & Gentry: Van Devender 93-483.

J. pilosella (Nees) Hilsenb.: Breedlove 69439.

J. pringlei B. L. Rob.: Breedlove & Strother 46783.

J. purpusii (Brandegge) D. N. Gibson: Moran 6941.

J. ramosa (Oerst.) V. A. W. Graham: Daniel & Baker 3778.

J. rzedowskii (Acosta) T. F. Daniel: Ventura & Lopez 1074.

J. salviiflora Kunth: Breedlove & Raven 20133.

J. santelisiana Acosta & T. F. Daniel: Acosta C. 1276, Morton & Makrinius 2364.

- J. soliana* Standl.: Laughlin 2565.
J. spicigera Schldl.: Avila B. 28, Breedlove 9431.
J. tabascina T. F. Daniel: Cowan 2860.
J. teletheca T. F. Daniel: Breedlove 56314.
J. tianguensis T. F. Daniel: Breedlove 7365.
J. torresii T. F. Daniel: Torres C. 11472.
J. turipachensis T. F. Daniel: Breedlove 31242.
J. valvata T. F. Daniel: Contreras 9311, Dorantes et al. 3538, Vasquez T. et al. 2582.
J. warnockii B. L. Turner: Rowell 5131.
J. zopilotensis Henr. & Hiriart: Daniel 1192.
J. sp.: Breedlove 28247.
J. sp.: Cowan & Magaña 3138.
J. sp.: Martínez R. 403.
J. sp.: Lott & Bullock 2171.
J. sp.: Lott & Magallanes 443.
J. sp.: Lott et al. 3733.
J. sp.: Martínez R. 775.
J. sp.: Purpus 5850.
J. sp.: Salinas T. et al. 6624-a.
J. sp.: Torres B. 536.
J. sp.: Van Devender 94-54.
J. sp.: Wendt & Hernández 5727.
J. sp.: Wendt et al. 2994.
Rhytiglossa latifolia Nees: Cowan 1715.
Siphonoglossa mexicana Hilsenb.: Lott & Guadalupe A. 2656.

Lepidagathis Willd.

- L. alopecuroidea* (Vahl) R. Br. ex Griseb.: Daniel et al. 5461cv*, Martínez S. 18315.

Lophostachys Pohl

- L. chiapensis* Acosta: Breedlove 30873, Breedlove 66152.
L. soconuscana T. F. Daniel: Boege 1086.
L. uxpanapensis Acosta: Hernández G. 642.

Louteridium S. Watson

- L. brevicalyx* A. T. Richardson: Hinton 15843.
L. donnell-smithii S. Watson: Breedlove 57578.
L. mexicanum (Baill.) Standl.: Breedlove 30786, Breedlove & Daniel 70879gh.
L. parayi Miranda: Breedlove 70889.
L. purpusii Brandege: Breedlove 31613.
L. rzedowskii T. F. Daniel: Kruse 1380.
L. tamaulipense A. T. Richardson: Hutchinson s.n.

Mendoncia Vell. ex Vand.

- M. guatemalensis* Standl. & Steyer M.: Hernández G. 1140.
M. retusa Turrill: Daniel s.n.*, Matuda 16603.

Mexacanthus T. F. Daniel

- M. mcvaughii* T. F. Daniel: Daniel 2107, McVaugh 23016.

Mirandea Rzed.

- M. andradenia* T. F. Daniel: Daniel & Baker 3693.
M. grisea Rzed.: Daniel 331, Daniel 852.
M. huastecensis: Daniel 252, Daniel & Baker 3616.
M. sylvatica Acosta: Wendt et al. 4104.

Nelsonia R. Br.

- N. canescens* (Lam.) Spreng.: Daniel et al. 5452*, Daniel et al. 5452cv*.

Odontonema Nees

- O. albiflorum* Leonard: Tellez & Villaseñor 6634.
O. auriculatum (Rose) T. F. Daniel: Daniel & Bartholomew 4913.
O. callistachyum (Schldl. & Cham.) Kuntze: Daniel & Bartholomew 5014.
O. cuspidatum (Nees) Kuntze: Breedlove & McClintock 23784, Dwyer 2076.
O. glaberrimum (M. E. Jones) V. M. Baum: Breedlove 49628.
O. glabrum Brandege: Breedlove & Bourell 67391.
O. mertonii V. M. Baum: Alexander 444.
O. tubaeforme (Bertol.) Kuntze: Daniel & Bartholomew 4991, Hoover 137.

Poikilacanthus Lindau

- P. capitatus* (Leonard) Ramamoorthy: Hinton 8075.
P. macranthus Lindau: Breedlove 26283, Breedlove 39887.
P. novogalicianus T. F. Daniel: McVaugh 15759.

Pseuderanthemum Radlk.

- P. alatum* (Nees) Radlk.: Daniel & Baker 3713.

- P. cuspidatum* (Nees) Radlk.: *Breedlove & Daniel* 70880.
P. fasciculatum (Oerst.) Leonard: *Ton* 903.
P. floribundum T. F. Daniel: *Daniel* 5381.
P. hispidulum (Nees) Radlk.: *Daniel* 6205.
P. pihuamoense T. F. Daniel: *Daniel et al.* 6283.
P. praecox (Benth.) Leonard: *Daniel* 2131, *McVaugh* 26541.
P. standleyi Leonard: *McVaugh* 23445, *Maya J.* 862.
P. verapazense Donn. Sm.: *Wendt et al.* 3113.
P. sp.: *Daniel & Ton* 6171.
P. sp.: *Camp* 2219.
P. sp.: *Clarke* 356.
P. sp.: *Daniel et al.* 5875gh.
- Ruellia* L.
- R. amoena* Sessé & Moc.: *Daniel & Butterwick* 3287.
R. bourgaei Hemsl.: *Rzedowski* 23294.
R. breedlovei T. F. Daniel: *Daniel & Bartholomew* 5025.
R. californica (Rose) I. M. Johnst.: *Daniel et al.* 6844, *Wiggins* 11411.
R. cedilloi Ramamoorthy: *Cedillo T. & Torres C.* 1425.
R. cordata Brandege: *Boyd & Ross* 5934.
R. eumorphantha Lindau: *Daniel & Bartholomew* 4927.
R. foetida Willd.: *Daniel* 2081gh.
R. fruticosa Sessé & Moc.: *Daniel & Jessup* 5776.
R. geminiflora Kunth: *Breedlove* 9163.
R. guerrerensis T. F. Daniel: *Hinton* 11296.
R. harveyana Stapf: *Hernández G.* 447.
R. hirsutoglandulosa (Oerst.) Hemsl.: *Daniel & Baker* 3736.
R. hookeriana (Nees) Hemsl.: *Breedlove & Daniel* 71060.
R. intermedia Leonard: *Jenkins et al. s.n.*
R. inundata Kunth: *Daniel & Butterwick* 6952, *Daniel et al.* 3315.
R. jaliscana Standl.: *Daniel & Bartholomew* 4855.
R. jussieuoides Schldtl. & Cham.: *Breedlove & Almeda* 57192.
R. lactea Cav.: *Tenorio L. & Romero de T.* 6720.
R. leucantha Brandege: *Daniel & Butterwick* 6940, *Brandegee s.n.*
R. matagalpae Lindau: *Breedlove & Daniel* 70899.
- R. matudae* Leonard: *Breedlove & Almeda* 57020.
R. maya T. F. Daniel: *Daniel & Bartholomew* 5000.
R. mcvaughii T. F. Daniel: *Cowan* 4746.
R. megasphaera Lindau: *Breedlove* 56280.
R. novogaliciana T. F. Daniel: *Hinton* 12931.
R. nudiflora (Engelm. & A. Gray) Urb.: *Wiggins & Rollins* 136.
R. paniculata L.: *Breedlove & McClintock* 23447.
R. parryi A. Gray: *Daniel* 247.
R. pereducta Standl. ex Lundell: *Davidse et al.* 20405.
R. petiolaris (Nees) T. F. Daniel: *Daniel & Bartholomew* 4930.
R. pringlei Fernald: *Torres C. et al.* 226.
R. puberula Leonard: *Salinas T. et al.* 6898.
R. speciosa (Nees) Lindau: *Pringle* 13155.
R. stemonacanthoides (Oerst.) Hemsl.: *Daniel & Bartholomew* 4871.
- Sanchezia* Ruiz & Pav.
- S. parvibracteata* Sprague & Hutch.: *Breedlove & Daniel* 71315.
S. speciosa Leonard: *Rosas R.* 1261.
- Schaueria* Nees
- S. parviflora* (Leonard) T. F. Daniel: *Contreras* 11180, *Herrera* 72, *Trigos* 198.
- Spathacanthus* Baill.
- S. hahnianus* Baill.: *Breedlove & Smith* 21618, *Hernández G.* 1777, *Hernández G. & González L.* 1855, *Wendt et al.* 2769.
S. parviflorus Leonard: *Matuda* 1696, *Ramírez-Marcial & Quintana-Ascencio* 507, *Skutch* 961*, *Steyermark* 46632*.
- Staurogyne* Wallich
- S. agrestis* Leonard: *Lott et al.* 3226, *Lott et al.* 3396.
- Stenandrium* Nees
- S. barbatum* Torr. & A. Gray: *Johnston et al.* 10589.5.
S. chameranthemoideum Oerst.: *Breedlove* 67020.
S. dulce (Cav.) Nees: *Angeles* 2, *Breedlove & Almeda* 45287, *Chiang et al.* 8198, *Hernández M.* 5995, *Hinton* 6086, *Padilla* 8, *Standley* 71*.

- S. manchonense* T. F. Daniel: *Hinton 10460*.
S. nanum (Standl.) T. F. Daniel: *Cabrera 1470*.
S. pedunculatum (Donn. Sm.) Leonard: *Bullock 1366*.
S. pilosulum (Blake) T. F. Daniel: *Moran 21965*.
S. subcordatum Standl.: *Chater et al. 3*.
S. verticillatum Brandegee: *Purpus 3939*.

Stenostephanus Nees

(including taxa for which nomenclatural combinations have not been published)

- S. breedlovei* T. F. Daniel: *Breedlove 49644*.
S. chiapensis T. F. Daniel: *Breedlove 34374*.
S. glaber (Leonard) T. F. Daniel: *Cloud 4*.
S. gracilis (Oerst.) T. F. Daniel: *Breedlove 71524*.
S. latilabris (D. N. Gibson) T. F. Daniel: *Matuda 2485*.
S. monolophus (Donn. Sm.) T. F. Daniel: *Breedlove & Smith 22692*.
S. purpusii (Brandegee) T. F. Daniel: *Purpus 6824*.
S. silvaticus (Nees) T. F. Daniel: *Zuill 772*.
S. tacanensis (Acosta & R. Fernández) T. F. Daniel: *Breedlove & Almeda 47714*.
S. sp.: *Reko 3724*.
S. sp.: *MacDougall s.n.*
S. sp.: *Hinton 10758*.
S. sp.: *Breedlove 72407*.
S. sp.: *Campos V. 4736*.
S. sp.: *Breedlove 36060*.
S. sp.: *Breedlove 61946*.
Habracanthus haematodes Nees: *Ventura A. 20491*.
Habracanthus harleyi Wassh.: *Reveal et al. 4239*.

Tetramerium Nees

- T. abditum* (Brandegee) T. F. Daniel: *Daniel 3364, Gentry 1178*.

- T. butterwickianum* T. F. Daniel: *Daniel & Butterwick 3267*.
T. crenatum T. F. Daniel: *Morton & Makrinius 2680*.
T. diffusum Rose: *Daniel 1141, Daniel 2097*.
T. emilyanum T. F. Daniel: *Daniel & Butterwick 3258*.
T. fruticosum Brandegee: *Daniel & Butterwick 6869, Daniel et al. 2490gh*.
T. glandulosum Oerst.: *Daniel 2104, Daniel 2104gh*.
T. glutinosum Lindau: *Daniel et al. 3342*.
T. guerrerense T. F. Daniel: *Hinton 11000*.
T. langlassei Happ: *Daniel et al. 3310gh*.
T. mcvaughii T. F. Daniel: *Daniel & Butterwick 3247*.
T. nemorum Brandegee: *Ventura A. 12283*.
T. nervosum Nees: *Carter & Moran 5324, Daniel 117*, Daniel 3443*.
T. oaxacanum T. F. Daniel: *Fryxell & Lott 3390*.
T. obovatum T. F. Daniel: *MacDougall s.n.*
T. ochoterena (Miranda) T. F. Daniel: *González Q. 3631*.
T. rubrum Happ: *Daniel & Butterwick 3270, Daniel et al. 3301*.
T. rzedowskii T. F. Daniel: *Daniel & Butterwick 3254*.
T. tenuissimum Rose: *Daniel 3384*.
T. yaquianum T. F. Daniel: *Daniel 3372*.

Thunbergia Retz.

- T. alata* Bojer ex Sims: *Daniel s.n.**.
T. erecta (Benth.) T. Anders.: *Ton 6367*.
T. fragrans Roxb.: *Daniel & Butterwick 6641gh**.
T. grandiflora Roxb.: *Breedlove 20052*.

Yeatesia Small

- Y. mabryi* Hilsenb.: *Daniel & Baker 3698*.
Y. platystegia (Torr.) Hilsenb.: *McCart 7445, Peterson 1313*.

FIGURE LEGENDS

FIGURE 1. Pollen of Thunbergioideae, Mendoncioideae, and Nelsonioideae. a. *Thunbergia fragrans* (Daniel & Butterwick 6641gh), equatorial view; b. *T. alata* (Daniel s.n.), equatorial view; c. *T. alata* (Daniel s.n.), polar view; d. *T. erecta* (Ton 6367), equatorial view; e. *Mendoncia retusa* (Matuda 16603), equatorial view; f. *M. guatemalensis* (Hernández G. 1140), polar view; g. *Elytraria mexicana* (Daniel & Butterwick 3263gh), polar view; h. *E. imbricata* (Porter 297), intercolpal view; i. *Nelsonia canescens* (Daniel et al. 5452), colpal view; j. *Staurogyne agrestis* (Lott 3226), colpal view. Scale for a–d = 43 μ m; for e, f = 36 μ m; for g, h = 29 μ m; for i = 22 μ m; for j = 14 μ m.

FIGURE 2. Pollen of Aphelandreae. a. *Aphelandra gigantiflora* (Breedlove 70900), colpal view; b. *Holographis tamaulipica* (Woodruff et al. 166), polar view; c. *A. schiedeana* (Ventura A. 12241), intercolpal view; d. *H. virgata* (Carter & Ferris 3819), intercolpal view; e. *Stenandrium dulce* (Breedlove & Almeda 45287), intercolpal view; f. *S. verticillatum* (Purpus 3939), colpal view; g. *S. dulce* (Hinton 6086), interapertural view; h. *S. barbatum* (Johnston et al. 10589.5), interapertural view; i. *S. dulce* (Standley 71). Scale for a, d–i = 22 μ m; for b = 14 μ m; for c = 29 μ m.

FIGURE 3. Pollen of Louteridieae and Trichanthereae. a. *Louteridium mexicanum* (Breedlove 30786); b. *Bravaisia integerrima* (Daniel 2144), colpal view; c. *B. grandiflora* (Daniel & Bartholomew 4998), intercolpal view; d. *Sanchezia parvibracteata* (Breedlove & Daniel 71315), colpal view; e. *S. speciosa* (Rosas R. 1261), intercolpal view. Scale for a = 72 μ m; for b = 29 μ m; for c–e = 43 μ m.

FIGURE 4. Pollen of Petalidiinae and Hygrophilinae. a. *Dyschoriste pringlei* (Villa C. & Chávez L. 755), intercolpal view; b. *D. pringlei* (Villa C. & Chávez L. 755), polar view; c. *D. decumbens* (Jones 24437), colpal view; d. *Hygrophila costata* (Wendt 3109), polar view; e. *H. costata* (Daniel et al. 8163cv), colpal view. Scale for a–c = 29 μ m; for d, e = 22 μ m.

FIGURE 5. Pollen of Ruelliinae, Barleriinae, Blechninae, and Lepidagathideae. a. *Ruellia inundata* (Daniel & Butterwick 6952), apertural view; b. *R. pringlei* (Torres C. et al. 226), interapertural view; c. *R. intermedia* (Jenkins et al. s.n.), probable polar view; d. *Lophostachys uxpanapensis* (Hernández G. 642), intercolpal view; e. *Barleria oenotheroides* (Daniel et al. 8412), apertural view; f. *B. oenotheroides* (Daniel 5327), polar view; g. *L. uxpanapensis* (Hernández G. 642), colpal view; h. *Blechnum pyramidatum* (Daniel et al. 5454), polar view; i. *Lepidagathis alopecuroides* (Martínez S. 18315), colpal view. Scale for a–c = 43 μ m; d, g = 36 μ m; e, f = 62 μ m; h = 29 μ m; i = 11 μ m.

FIGURE 6. Pollen of Isoglossinae and Poikilacanthus. a. *Stenostephanus gracilis* (Breedlove 71524), apertural view; b. *S. gracilis* (Breedlove 71524), interapertural view; c. *S. chiapensis* (Breedlove 34374), apertural view; d. *S. chiapensis* (Breedlove 34373), interapertural view; e. *Poikilacanthus novogalicianus* (McVaugh 15759), oblique view; f. *P. macranthus* (Breedlove 39887), polar view. Scale for a–d = 29 μ m; for e, f = 36 μ m.

FIGURE 7. Pollen of Odontoneminae. a. *Dicliptera resupinata* (Daniel et al. 6865), intercolpal view; b. *Tetramerium fruticosum* (Daniel & Butterwick 6869), colpal view; c. *Hoverdenia speciosa* (Rzedowski 36934), colpal view. d. *Aphanosperma sinaloensis* (Van Devender et al. 93-1494), intercolpal view; e. *A. sinaloensis* (Daniel 4070), polar view; f. *Pseuderanthemum floribundum* (Daniel 5381), polar view; g. *Gypsacanthus nelsonii* (Trejo V. 390), colpal view; h. *Schaueria parviflora* (Trigos 198), colpal view; i. *Chileranthemum pyramidatum* (Breedlove 27655), colpal view; j. *Yeatesia platystegia* (Peterson 1313), intercolpal view. Scale for a, d, e = 22 μ m; for b, g = 14 μ m; for c, f = 36 μ m; for h–j = 29 μ m.

FIGURE 8. Pollen of Odontoneminae. a. *Chalarothyrsus amplexicaulis* (Daniel & Bartholomew 4842), intercolpal view; b. *Henrya tuberculosperra* (Daniel & Bartholomew 4868), intercolpal view; c. *Carlwrightia arizonica* (Daniel et al. 6845), colpal view; d. *Mexacanthus mcvaughii* (McVaugh 23016), intercolpal view. e. *Aphanosperma sinaloensis* (Daniel et al. 6866), colpal and subpolar

views; f. *Anisacanthus pumilis* (Lott & Magallanes 313), polar view; g. *Spathacanthus hoffmannii* (Skutch 325), polar view; h. *Mirandea grisea* (Daniel 852), polar view; i. *Odontonema cuspidatum* (Breedlove & McClintock 23784), polar view. Scale for a, i = 29 μm ; for b = 23 μm ; for c, e, f, h = 22 μm ; for d, g = 36 μm .

FIGURE 9. Pollen of Justiciinae. a. *Justicia tabascina* (Cowan 2860), apertural view; b. *J. medranoi* (Daniel & Baker 3742), apertural view; c. *J. breedlovei* (Breedlove 56242), interapertural view; d. *J. ixtlania* (Daniel 2070), apertural view; e. *J. fulvicoma* (Daniel & Baker 3637), apertural view; f. *J. zopilotensis* (Daniel 1192), polar view; g. *J. angustiflora* (Reyes 1255), apertural view; h. *J. angustiflora* (Reyes 1255), polar view; i. *J. fulvicoma* (Daniel & Baker 3637), polar view. Scale for a, b, d, e, g–i = 29 μm ; for c = 22 μm ; for f = 32 μm .

FIGURE 10. Pollen of Justiciinae. a. *Justicia masiaca* (White 3590), apertural view; b. *J. candicans* (Moran 18787), apertural view; c. *J. jitotolana* (Thorne & Lathrop 41662), interapertural view; d. *J. aurea* (Breedlove 29496), apertural view; e. *J. soliana* (Laughlin 2565), interapertural view; f. *J. warnockii* (Rowell 5131), apertural view; g. *J. warnockii* (Rowell 5131), polar view; h. *J. clinopodium* (Daniel et al. 5873), apertural view; i. *J. breviflora* (Breedlove 50689), apertural view. Scale for a, b, e, h = 29 μm ; for c = 36 μm ; for d = 43 μm ; for f, g = 14 μm ; for i = 22 μm .

FIGURE 11. Exine surfaces. a. *Mendoncia retusa* (Matuda 16603); b. *Elytraria bromoides* (Daniel 303); c. *Nelsonia canescens* (Daniel et al. 5452); d. *Louteridium purpusii* (Breedlove 31613); e. *Dyschoriste capitata* (Breedlove 26151); f. *Hygrophila costata* (Daniel et al. 8163); g. *Blechnum pyramidatum* (Daniel et al. 5454); h. *Ruellia novogaliciana* (Hinton 12931); i. *Hypoestes phyllostachya* (Breedlove & Daniel 70764). Scale for a, c, i = 2.1 μm ; for b = 2.7 μm ; for d = 10.7 μm ; for e–g = 3.1 μm ; for h = 5.4 μm .

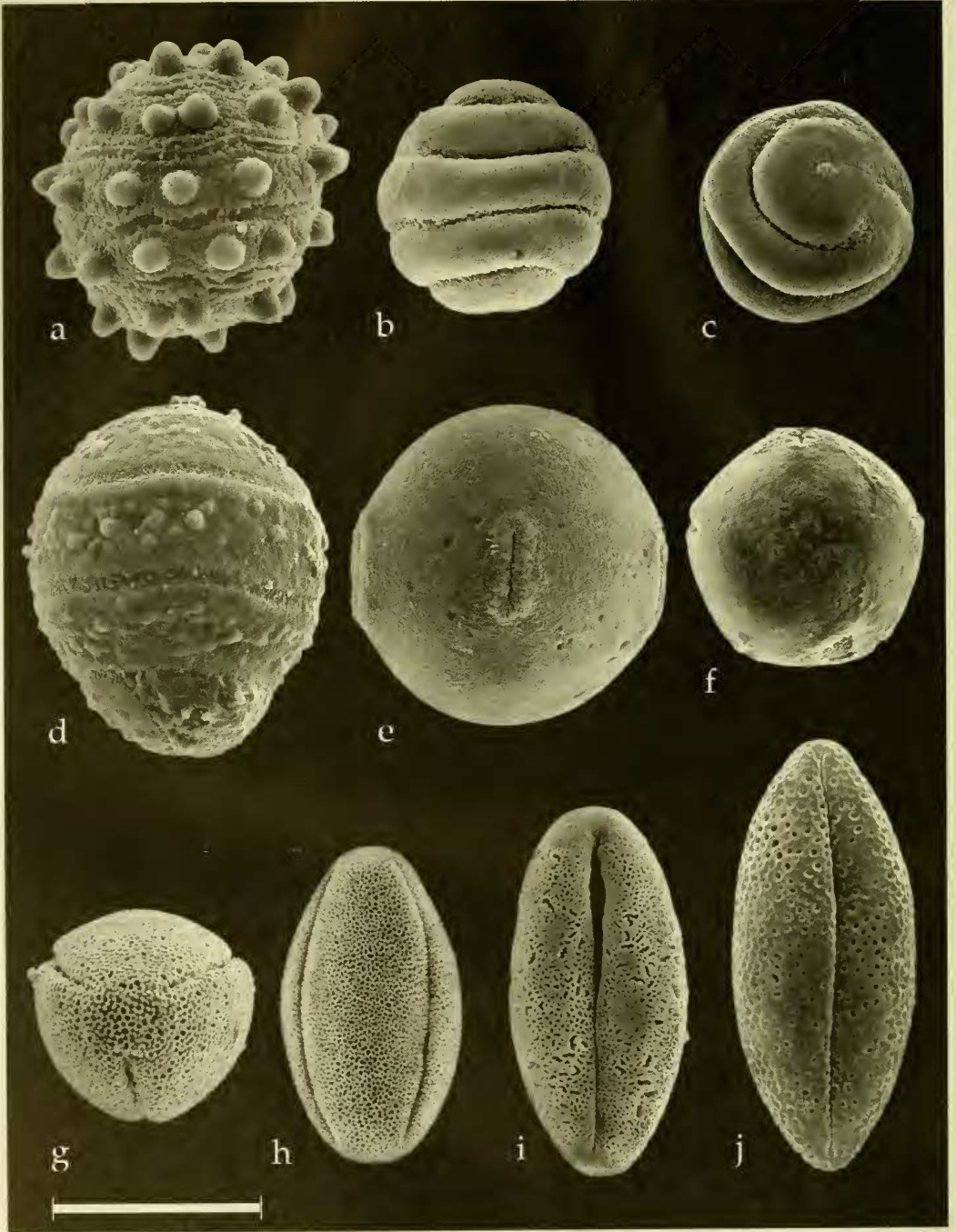


FIGURE 1

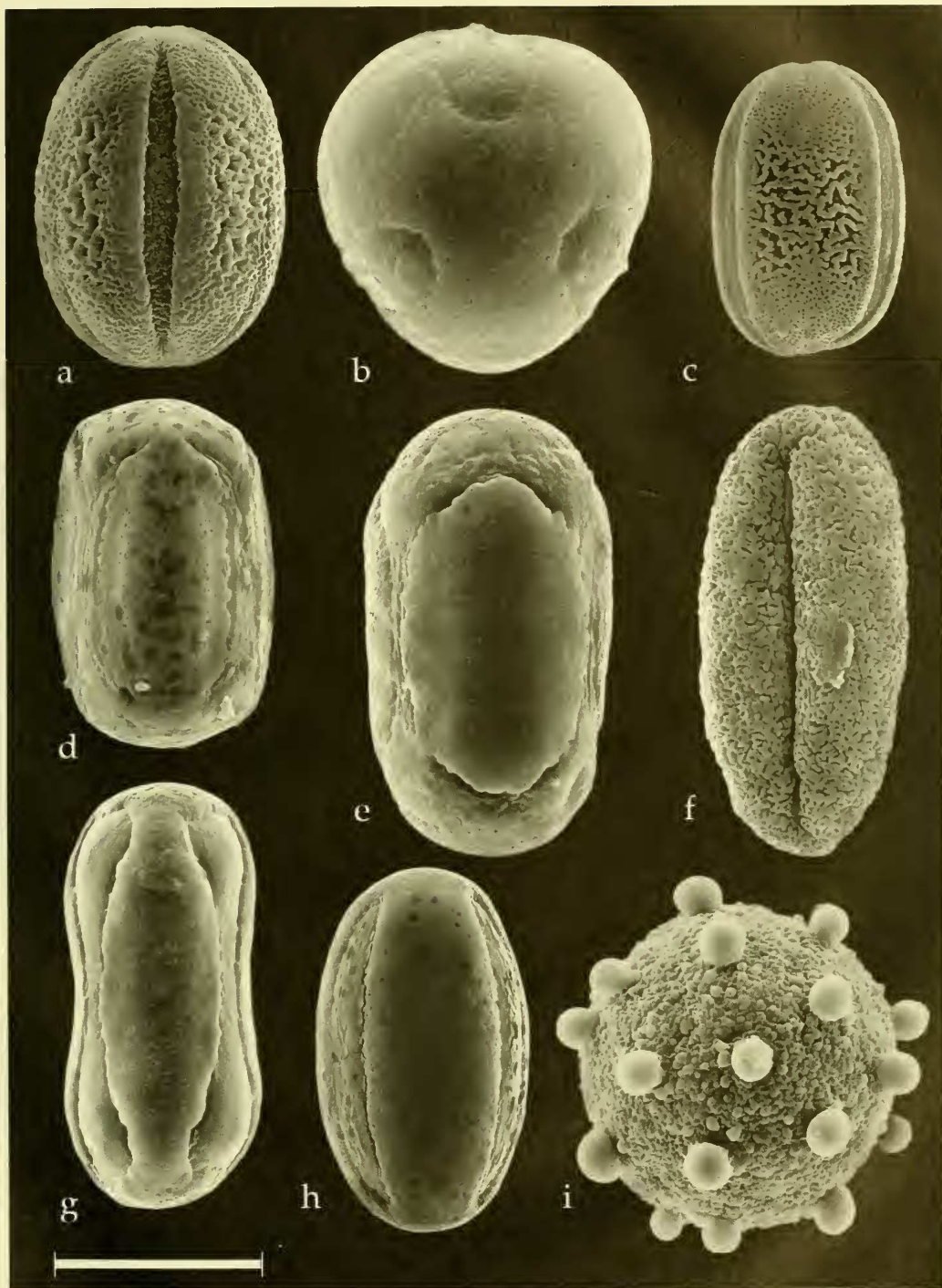


FIGURE 2

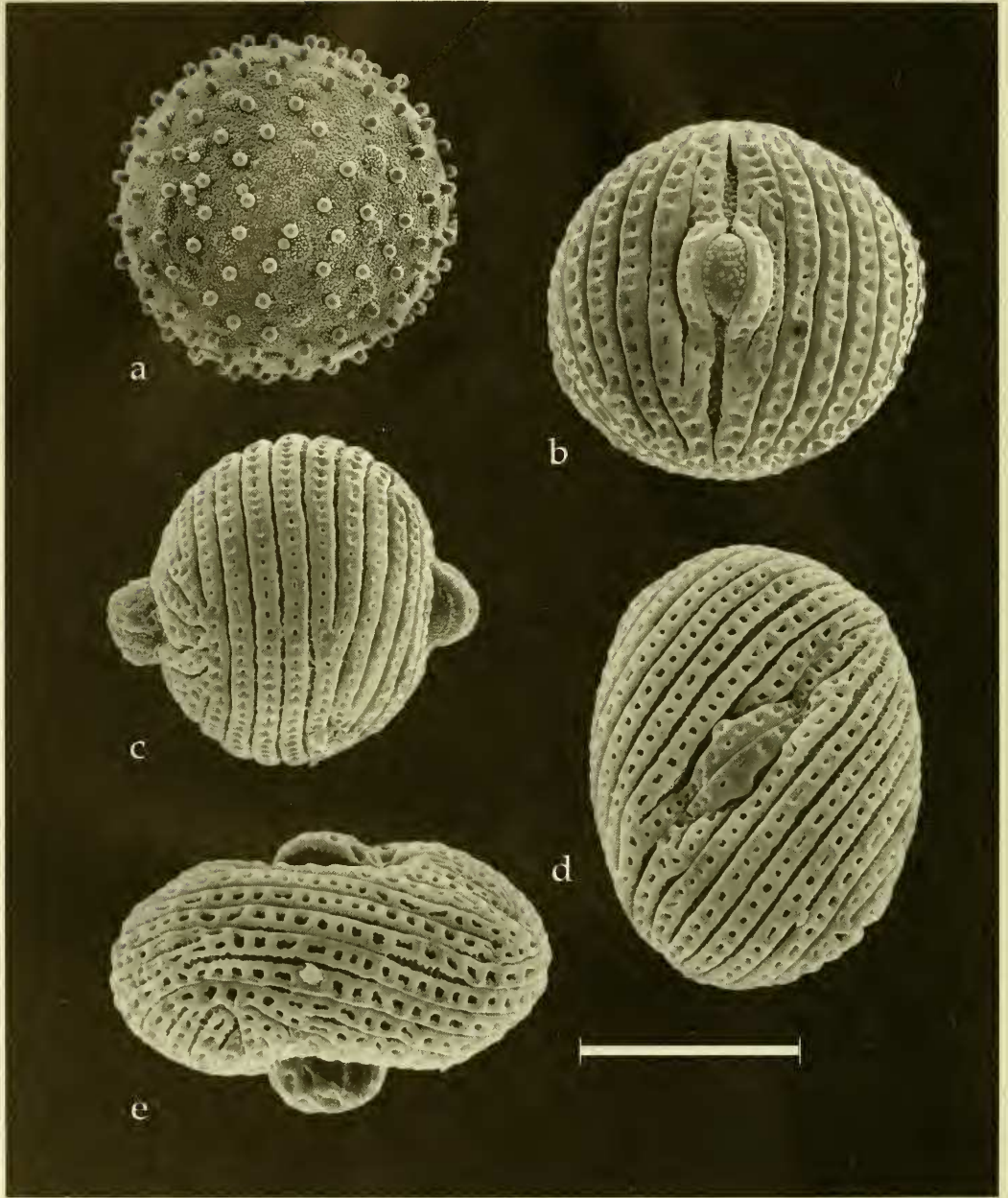


FIGURE 3

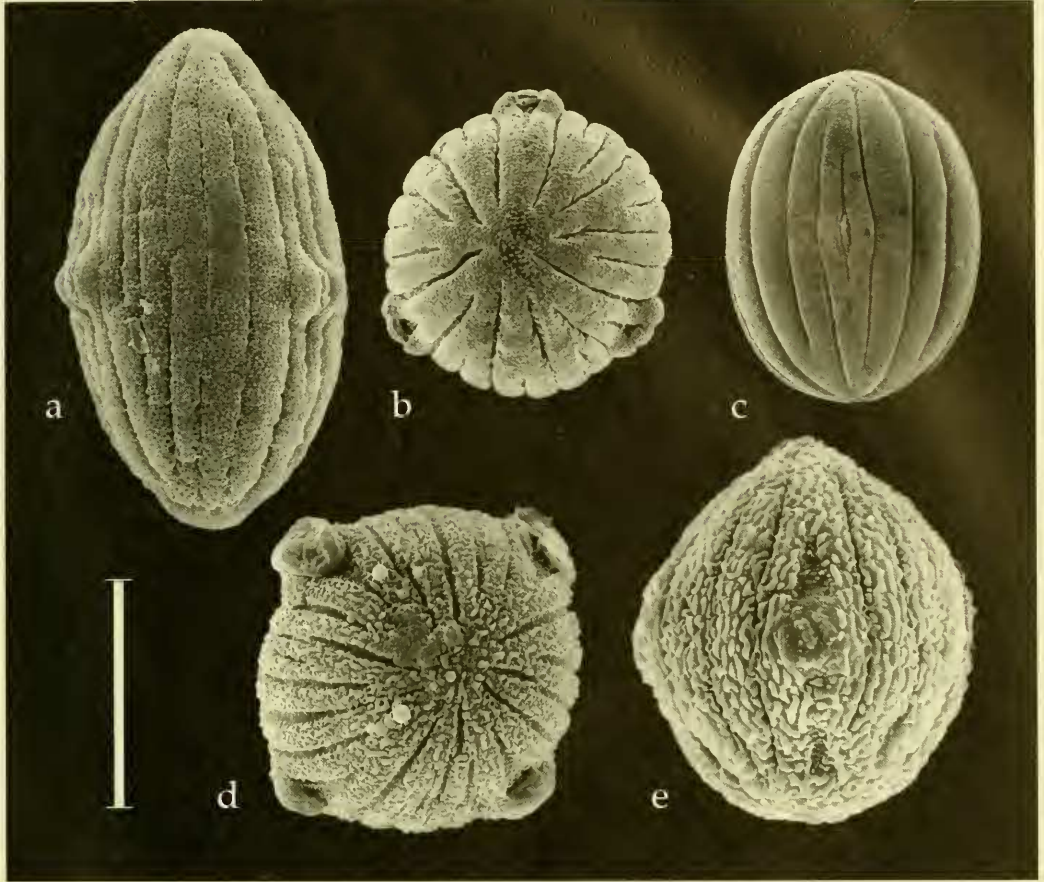


FIGURE 4

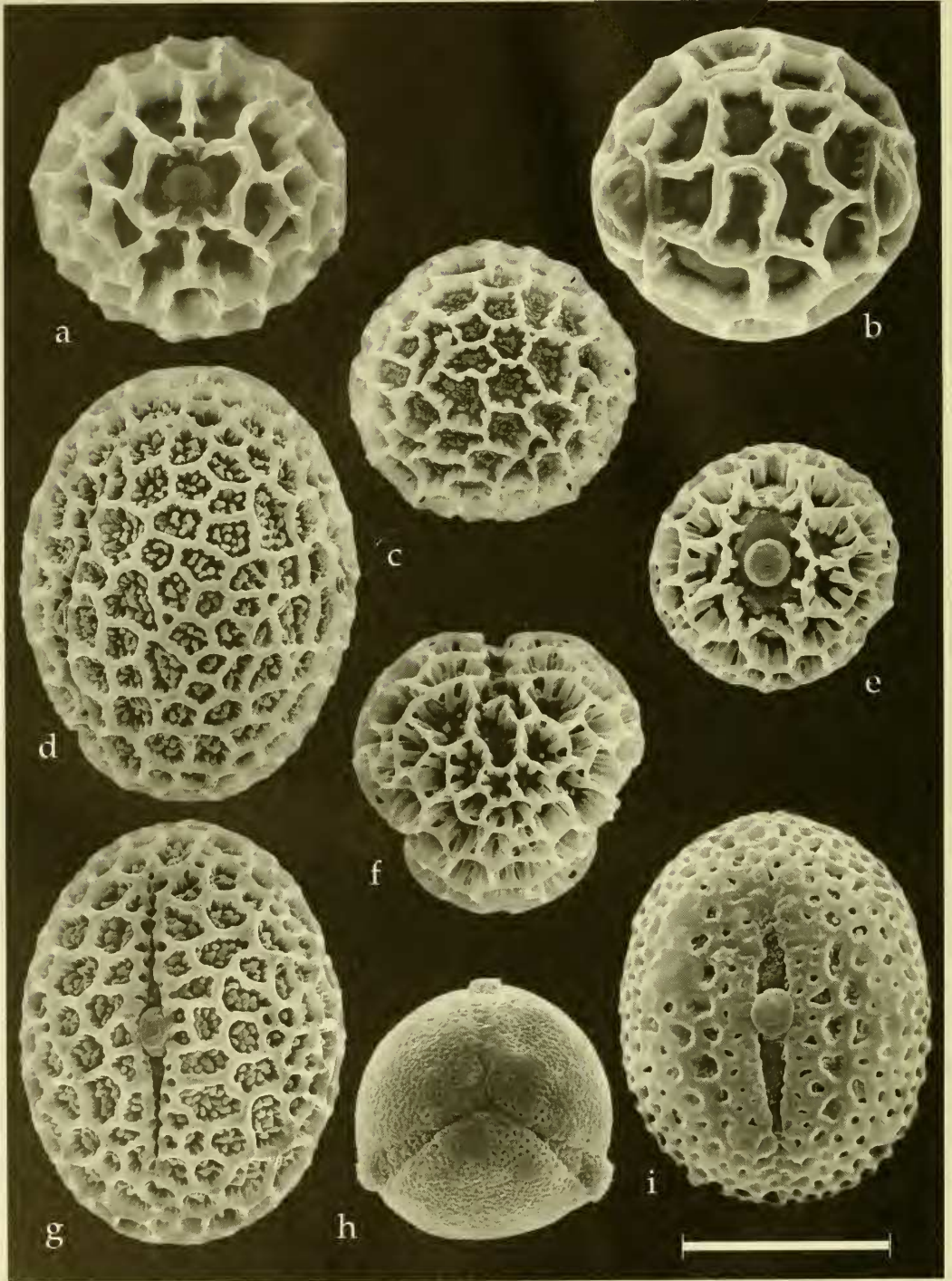


FIGURE 5

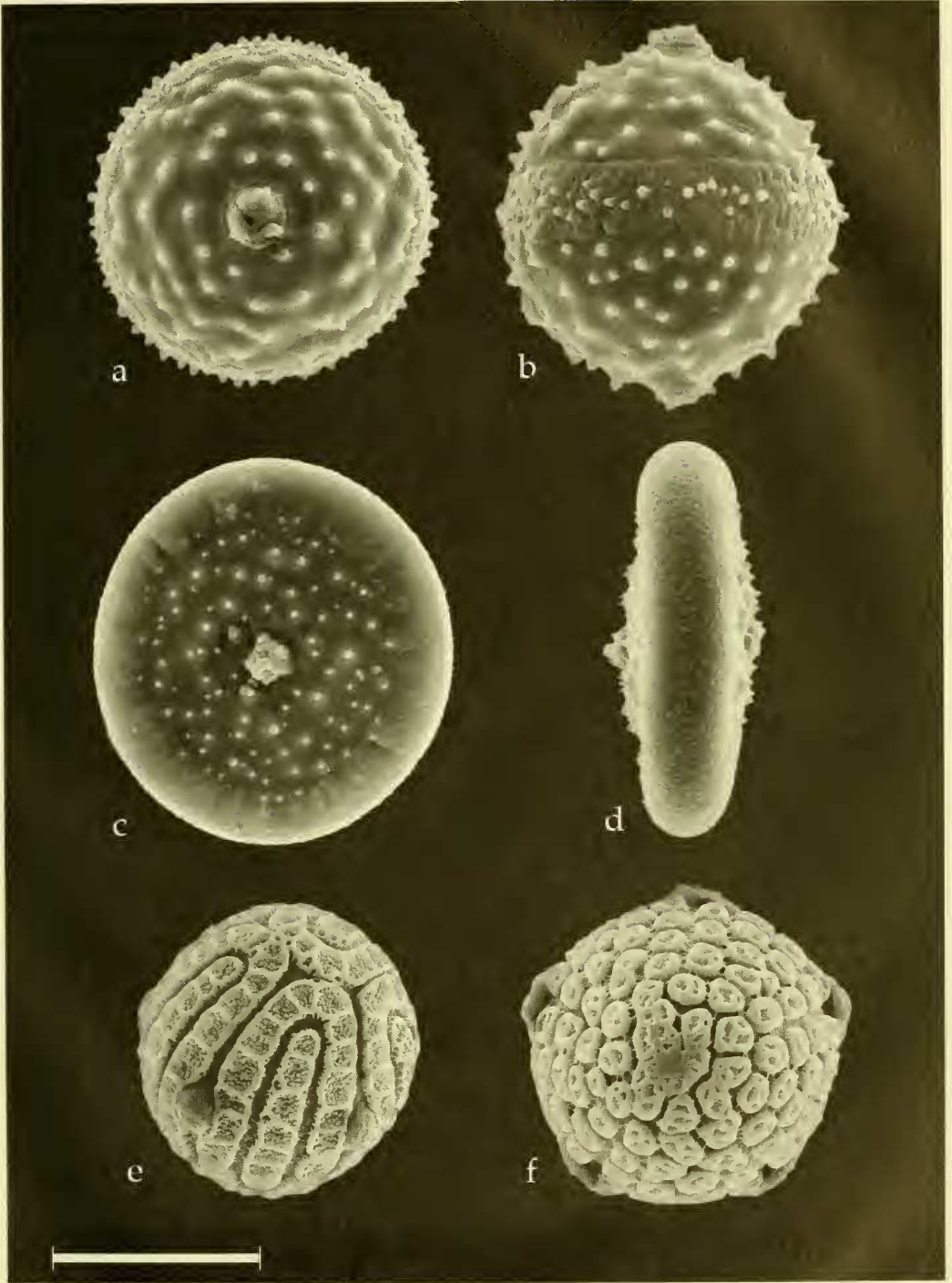


FIGURE 6

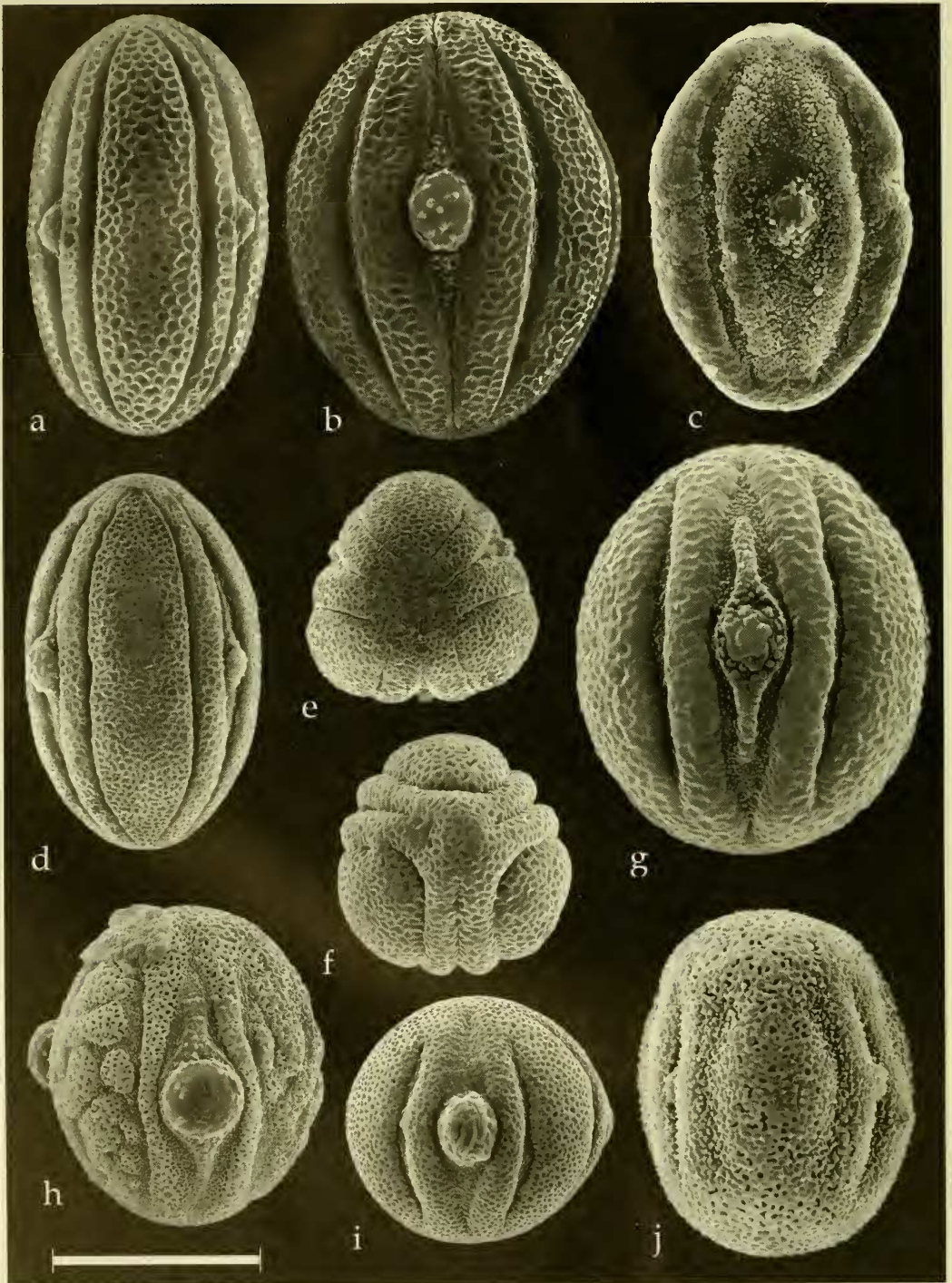


FIGURE 7

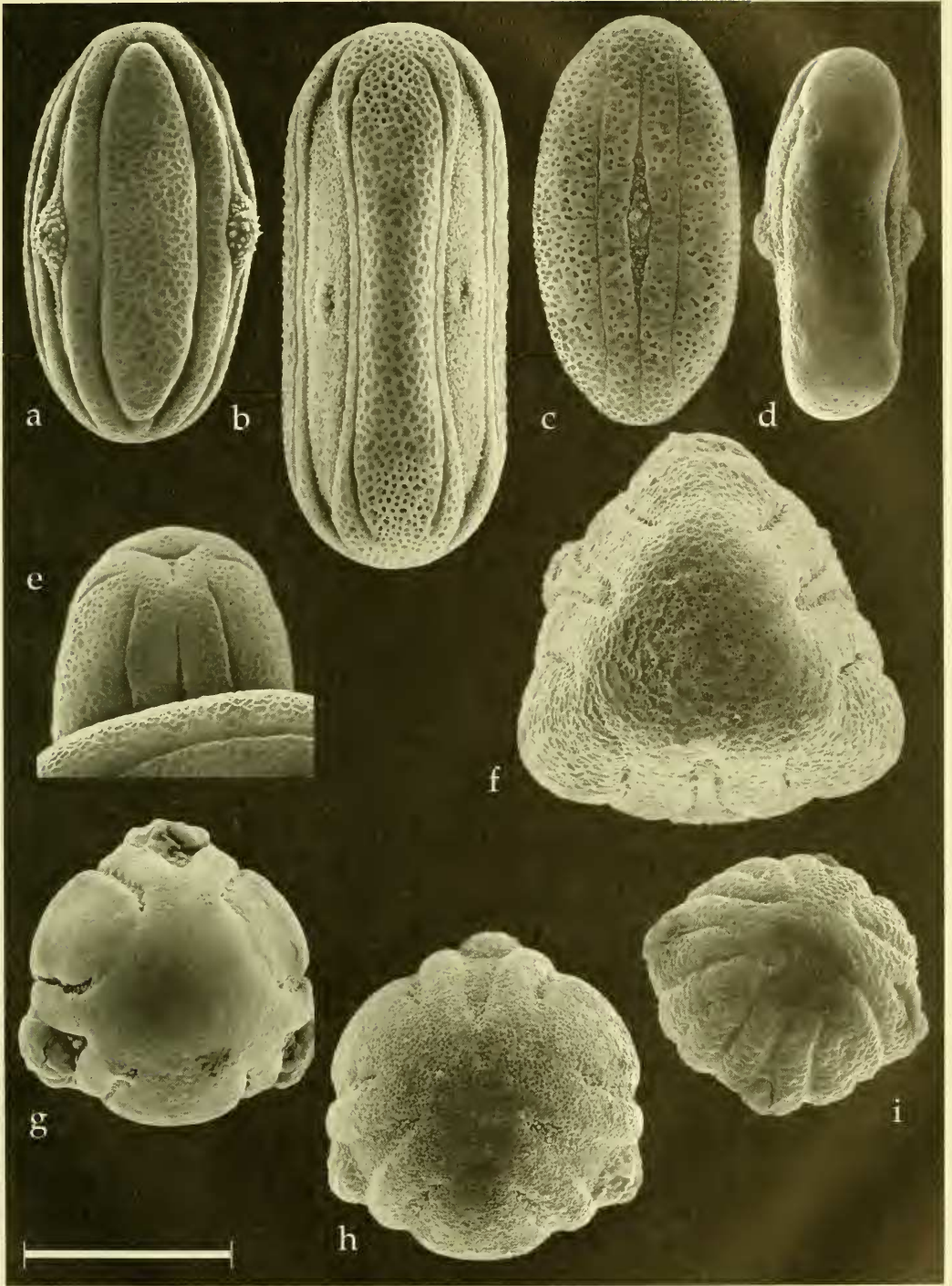


FIGURE 8

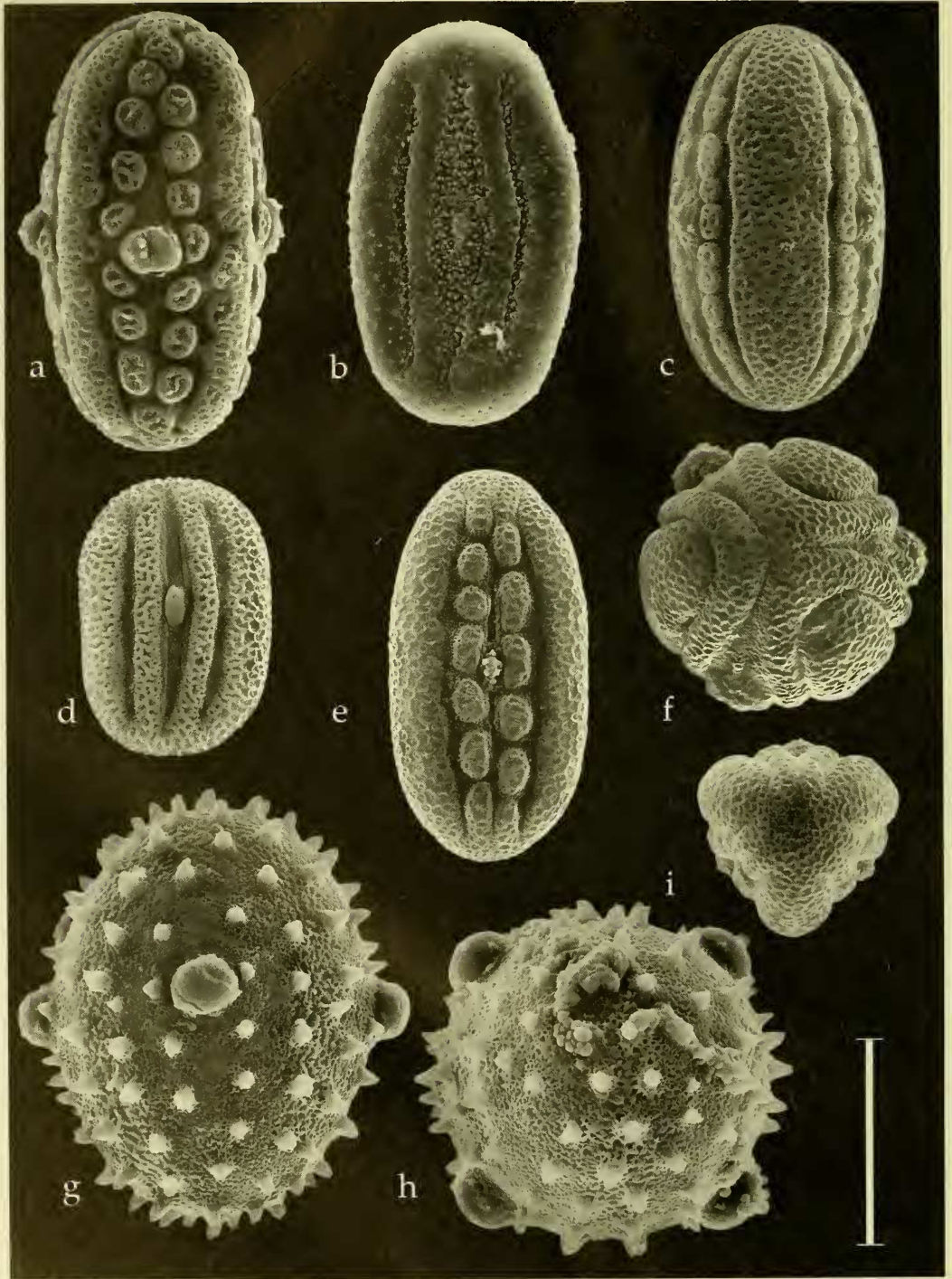


FIGURE 9

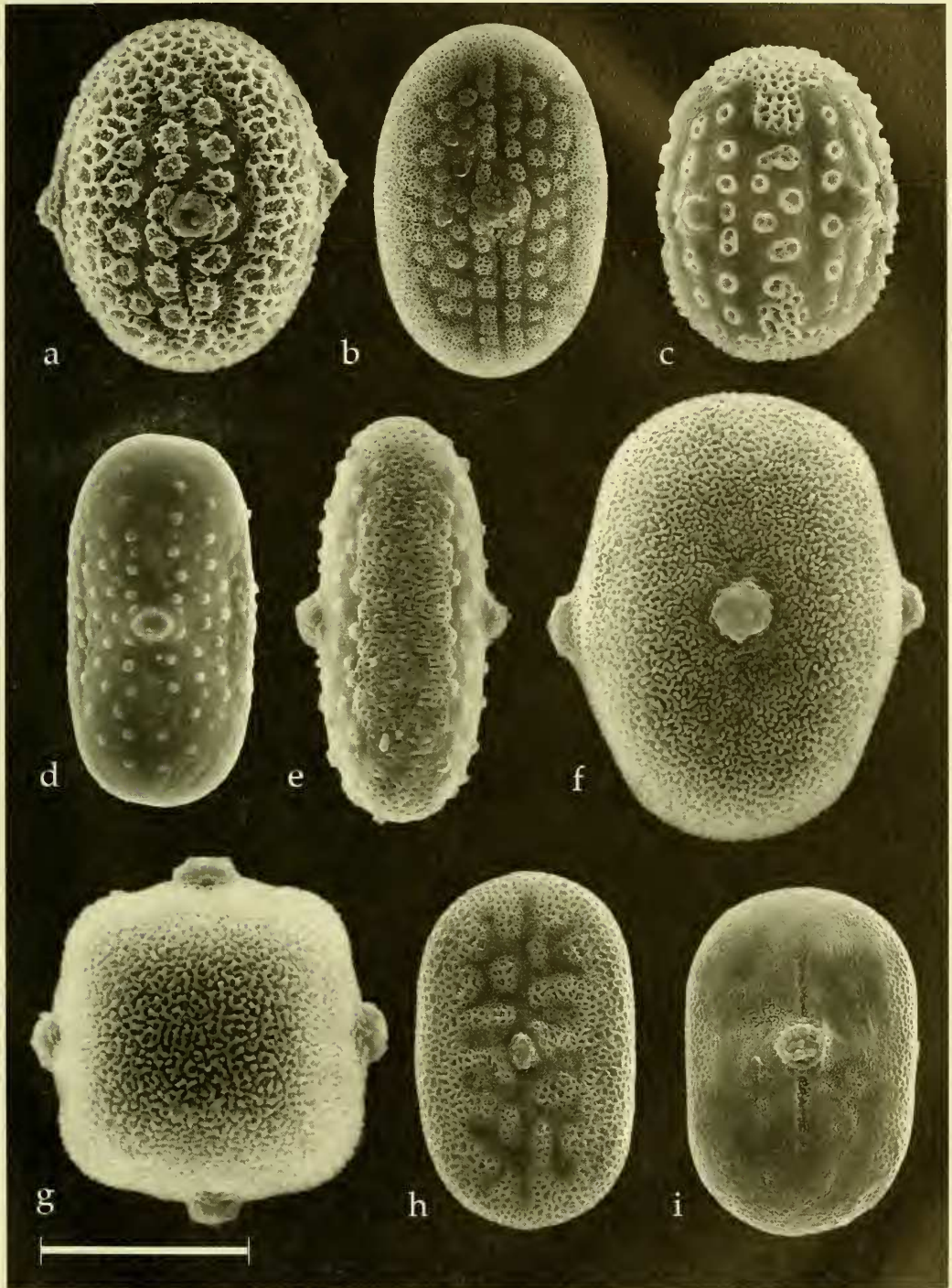


FIGURE 10

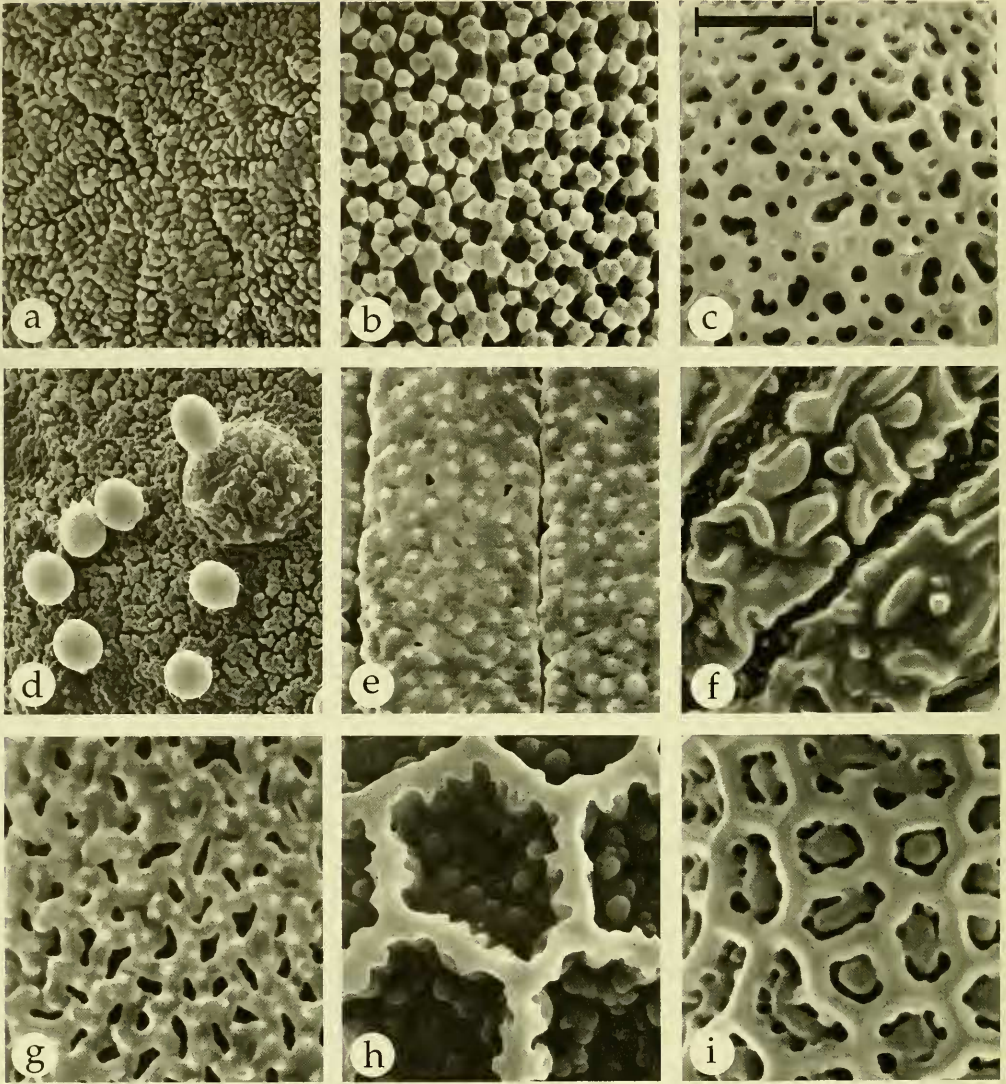


FIGURE 11